EVIDENCE OF NICHE SIMILARITY BETWEEN CUTTHROAT TROUT (*Oncorhynchus clarkii*) AND BROOK TROUT (*Salvelinus fontinalis*): IMPLICATIONS FOR DISPLACEMENT OF NATIVE CUTTHROAT TROUT BY NONNATIVE BROOK TROUT

by

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DEDICATION

I dedicate this dissertation to my wife, Mary E. Lennon, and our two children, Ben and Madison, who supported me tirelessly through the pursuit of this degree. Words cannot adequately express my gratitude. I also thank God whom I believe led me to this degree so that I could more fully understand my need for both faith and science in the pursuit of truth. “Science without religion is lame. Religion without science is blind.” (Albert Einstein, "Science, Philosophy and Religion: a Symposium", 1941).

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ABSTRACT

To evaluate whether nonnative brook trout, *Salvelinus fontinalis*, and native westslope cutthroat trout, *Oncorhynchus clarkii lewisi*, occupied a similar niche I developed and evaluated finite population correction factor (FPC) methods for estimating fish biomass in small streams (< 5 m wide). These new FPC methods take advantage of the fact that relatively high proportions of the total population are captured and can be measured and weighed during removal population estimation. Biomass estimates for these FPC methods had much smaller coefficients of variation than the traditional method for both field and simulated data. Coverage by 95% confidence intervals for the FPC methods were much closer to the 95% nominal level than for the traditional method, especially when capture probabilities were higher than 0.5. Using simulated data, I found that removal population estimates deviated significantly from true population sizes, but that these deviations clustered near zero when the ratio of captured fish to the estimated number was 0.7 or higher.

Six to eleven multi-pass electrofishing efforts successfully eradicated nonnative brook trout from 1.7 to 3.0-km treatment reaches of four streams. Brook trout were eradicated to conserve native westslope cutthroat trout and evaluate competitive influences of brook trout on westslope cutthroat trout. Eradication success was related to stream size, distribution and abundance of brook trout, years of treatment, number of treatments per year, amount of cover, cover reduction efforts, and beaver ponds. Total trout biomasses significantly increased in all three streams after brook trout were eradicated, indicating that brook trout and cutthroat trout probably have similar niches and that interference competition may be occurring. Densities of juvenile and adult cutthroat trout were significantly ($P < 0.05$) and negatively affected by densities of juvenile and adult brook trout. I did not find a difference between cutthroat trout and brook trout density effects on body condition of cutthroat trout. I found evidence for size-asymmetric competition in one stream, but not in another. Interspecific competition between brook trout and cutthroat trout appeared to be as strong as intraspecific competition within cutthroat trout, providing insight into one mechanism by which brook trout might displace cutthroat trout.

Keywords: cutthroat trout, brook trout, interference competition, niche, biomass, finite population correction, removal population estimators, native trout, conservation, eradication of nonnative organisms, electrofishing, *Oncorhynchus clarkii lewisi*, *Salvelinus fontinalis*

CHAPTER 1

INTRODUCTION TO DISSERTATION

Behnke (1992) described the native inland trout of western North America and recognized 15 subspecies of cutthroat trout. Two of these subspecies, westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and Yellowstone cutthroat trout (*O. c. bouvieri*), occur in Montana (Brown 1971). The abundance and distribution of both of these subspecies have declined from historical levels throughout their respective ranges and genetically unaltered populations are estimated to currently occupy about 10% of their historical ranges (Hadley 1984; Liknes and Graham 1988; Varley and Gresswell 1988; Behnke 1992; McIntyre and Rieman 1995; Gresswell 1995; Van Eimeren 1996; Shepard et al. 1997; Kruse et al. 2000; May et al. 2003; Shepard et al. 2005; Meyer et al. 2006; May et al. 2007). Factors associated with these declines include introductions of nonnative fishes, habitat changes, and over-exploitation (Hanzel 1959; Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995). I focused my research on resident forms of WCT that occupied headwater habitats in tributaries to the upper Missouri River within Montana.

Brook trout (*Salvelinus fontinalis*) now occupy many of the headwater habitats previously occupied by many of the subspecies of cutthroat trout (Behnke 1992; McIntyre and Rieman 1995) and they continue to invade and displace populations of native cutthroat trout (MacPhee 1966; Griffith 1972; Behnke 1979; Liknes and Graham 1988; Griffith 1988; Dunham et al. 2003). For invasion to be successful, individuals must not only be able to disperse, but habitats to which they disperse must be capable of supporting a reproducing population (Adams 1999; Dunham et al. 2002; Kennedy et al. 2003; Benjamin 2006; Benjamin et al. 2007). Brook trout appear to have flexible life histories that allow them to successfully inhabit a wide range of habitats from relatively warm, low elevation sites to cold, infertile, high elevation sites (Kennedy et al. 2003). Brook trout grew faster, matured earlier, and died earlier at moderate elevations than at high elevations (Kennedy et al. 2003). Age at maturity, but not growth, was inversely related to density of fish and intensity of interspecific competition for brook trout inhabiting lakes of the Canadian Shield area of southern Quebec (Magnan et al. 2005). This finding suggests that interspecific competition could lead to younger ages of reproduction for brook trout.

Invasion of brook trout into habitats occupied by native cutthroat trout offers an opportunity to study invasion ecology in the Northern Rocky Mountains of the western U.S. (Dunham et al. 2002). Studying ecological interactions during and following establishment of exotic species can provide insights into how invasion affects communities (Bohn and Amundsen 2001) and what managers might do to eliminate or reduce the risk of exotic invasion. Invasive species also offer excellent opportunities to study basic processes in population biology (Sakai et al. 2001).

Cutthroat trout, as well as many other native salmonids, were often restricted to high-elevation headwaters because of displacement by nonnative salmonids in lower-elevation reaches (Larson and Moore 1985; Fausch 1989; Paul and Post 2001; de la Hoz Franco and Budy 2005; McHugh and Budy 2005; McMahon et al. 2007). A pertinent question for those working to conserve native cutthroat trout populations is, “Do cutthroat trout and brook occupy a similar niche?” If so, can brook trout competitively exclude cutthroat trout from stream headwater habitats? If this is the case, conserving the remaining headwater native cutthroat trout populations may require physically isolating these headwater populations by construction of physical barriers (Propst et al. 1992; Harig et al. 2000; Hilderbrand and Kershner 2000; Hepworth et al. 2002; Novinger and Rahel 2003; Shepard et al. 2005; Peterson et al. 2008).

I first evaluated removal population estimators and developed an improved method for computing the variance of biomass estimates. Because removal estimators were used to evaluate populations of brook and cutthroat trout, it was important to understand the limitations and strengths of these estimators. I applied a finite population correction factor (FPC) for estimating variance of biomass estimates that can be used in conjunction with removal population estimates (Chapter 2). This new FPC method for estimating biomass variance takes advantage of the relatively high proportion of fish that are typically captured and weighed when conducting removal population estimates.

I posit that age-1 and older brook trout and cutthroat trout occupy functionally similar niches in headwater stream environments. I tested that hypothesis by removing brook trout from moderately long reaches (2 to 3 km) of several headwater streams and measuring the response of westslope cutthroat trout populations (Chapters 3 and 4). I evaluated the response of westslope cutthroat trout to removal of brook trout using estimates of biomass, fish condition, and densities. I investigated both species- and size-asymmetric competition effects.

Review of Literature

Cutthroat Trout

Westslope cutthroat trout historically occupied the broadest range of any cutthroat trout subspecies. The historical range of westslope cutthroat trout was a contiguous area encompassing the upper Missouri, upper Columbia (including the upper Salmon, upper Kootenai, upper Pend Oreille, and entire Clark Fork basins), and upper South Saskatchewan river basins, and several disjunct populations in the states of Washington and Oregon (Behnke 1992; Shepard et al. 2005). Westslope cutthroat trout populations have been displaced from many of their historical habitats by nonnative trout (Shepard et al. 1997; May et al. 2003; May et al. 2007). They appear especially sensitive to displacement by nonnative fish in larger streams and rivers and now often persist only in isolated headwater refuges, especially in the Missouri River basin (Shepard et al. 1997). Yellowstone cutthroat trout may be more resistant to displacement in larger rivers (May et al. 2003; DeRito 2004; May et al. 2007).

Cutthroat trout evolved under diverse conditions resulting in a high level of genetic and life history variability both among and within the subspecies (Shepard et al. 1984; Allendorf and Leary 1988; several papers in Gresswell 1988; Gresswell et al. 1997; Taylor et al. 2003; Wofford et al. 2005; Cegelski et al. 2006). The different life histories exhibited by cutthroat trout and estimates of their demographic rates have been widely reported (Miller 1953; Irving 1954; Ball and Cope 1961; Johnson 1963; Brown 1971; Behnke 1979; Lukens 1978; Gresswell 1988; Shepard et al. 1984; Bjornn and Liknes

1986; Liknes and Graham 1988; Varley and Gresswell 1988; Rieman and Apperson 1989; Bjornn and Reiser 1991; Downs et al. 1997; Meyer et al. 2003). As the genetic and life history variability exhibited by cutthroat trout is too broad to be encompassed within a single study, this research focused on "resident" forms of westslope cutthroat trout that remain in their natal tributaries through maturity.

Westslope cutthroat trout mature as early as age 3 (Brown 1971). Female westslope cutthroat trout typically mature during their third or fourth year, the majority of westslope cutthroat trout in most populations spawn at age 4 or age 5, and all individuals had spawned at least once by their sixth year (Behnke 1979; Bjornn and Liknes 1986; Rieman and Apperson 1989). Slow-growing resident populations probably spawn at similar ages as migratory populations, but at much smaller sizes because of their slower growth in higher elevation tributary streams (Thurow and Bjornn 1978; Rieman and Apperson 1989; Downs et al. 1997). In mid- to high-elevation streams in Montana, male stream-resident westslope cutthroat reached sexual maturity as early as age 2 and all males were sexually mature by age 4 whereas females first reached sexual maturity at about 150 mm (FL) and almost all females longer than 190 mm were sexually mature (Downs et al. 1997). Length was found to be a better predictor than age of sexual maturity in female stream-resident westslope cutthroat trout (Downs et al. 1997). The maximum age of stream-resident westslope cutthroat from several streams in Montana was determined to be 8 years based on interpretation of annuli in otoliths (Downs et al. 1997).

Fecundities estimated for westslope cutthroat trout ranged from about 200 to 2,000 eggs per female with the number of eggs related to size of females, usually in a linear or exponential fashion (Averett 1962; Johnson 1963; Smith et al. 1983; Downs et al. 1997; Wydoski 2003). Cutthroat trout typically spawned in the late spring and early summer and their fry often did not emerge until late-summer or early fall (Fleener 1951; Kaeding and Boltz 2001; Schmetterling 2001). At higher elevations where water temperatures are colder, cutthroat trout fry may emerge as late as late-August or early September. Cold water temperatures typically found at high elevations limited reproductive success of cutthroat trout in field and laboratory studies in Colorado (Coleman and Fausch 2007).

Westslope cutthroat trout have been found to use microhabitats with water velocities ranging from 0.1 to 0.3 m/sec (Griffith 1970,1972; Pratt 1984) and water deeper than the average available (Brown and Mackay 1995). The distribution and abundance of cutthroat trout have been strongly associated with the presence of pool habitats (Shepard 1983; Pratt 1984; Peters 1988; Hoelscher and Bjornn 1989; Heggenes et al. 1991; Ireland 1993; Young 1998). Young Colorado River cutthroat trout (*O. c. pleutiticus*) preferred pool habitats and used microhabitats where velocities were less than 0.03 m/sec and water was deeper than 3 cm (Bozek and Rahel 1991). Whereas Griffith (1970) and Pratt (1984) suggested that cutthroat trout prefer habitats that provide cover, Nakano et al. (1992) found that westslope cutthroat trout were found further from overhead cover than bull trout (*Salvelinus confluentus*) in a comparative study. Young-of-the-year coastal cutthroat trout (*O. c. clarki*) were found at stream margins and in backwaters and side channels in coastal mountain streams of Oregon (Moore and Gregory 1988), which I have observed for age-0 westslope cutthroat trout in Montana streams.

Brook Trout

The historical range of native brook trout extends from the Saskatchewan River to Hudson Bay and Labrador in Canada southward along the Appalachian Mountains to the state of Georgia and west to the upper Mississippi River system (MacCrimmon and Campbell 1969; Brown 1971). Brook trout have been widely stocked by fish management agencies throughout the western United States and are one of the most widespread nonnative species in this region (Fuller et al. 1999; Dunham et al. 2002). Brook trout were widely stocked in Montana from their first introduction into the Yellowstone River drainage in 1889 until 1954, when stocking was sharply reduced (Domrose 1963; Brown 1971; Figure 1.1). Brook trout established wild-reproducing populations at many of the locations where they were originally released and often dispersed from those sites to further colonize accessible and suitable habitats. Consequently, by 1970 Brown (1971) indicated that brook trout inhabited almost all Montana counties with waters suitable for trout.

Brook trout, much as cutthroat trout, have diverse life history strategies and high within-species variability (Power 2002; Angers et al. 1995; Dunham et al. 2002), probably because of the diverse conditions under which they evolved. Brook trout have the ability to disperse both upstream and downstream to colonize suitable habitats (Smith and Saunders 1958; Flick and Webster 1975; Erman 1986; Riley et al. 1992; Gowan and Fausch 1996; Adams 1999; Adams et al. 2000; Adams et al. 2001; Rodriguez 2002; Adams et al. 2002; Peterson and Fausch 2003a; Petty et al. 2005; Roghair 2005). They have been shown to successfully move upstream through short, steep reaches of stream (13% over 67 m long reaches and 22% over 14 m) and pass over vertical drops of up to 0.75 to 1.5 m (Adams 1999; Adams et al. 2000; Kondratieff 2004; Kondratieff et al. 2006). The exploratory migratory behavior exhibited by brook trout may have its evolutionary roots in the close association this species had with the continental ice sheets and their need to disperse during expansion and recession of these glacial ice sheets (Power 2002), a factor that also probably contributed to the migratory behavior of many northern Rocky Mountain cutthroat subspecies such as westslope cutthroat trout.

Female brook trout from a high-elevation stream in Colorado matured at lengths (FL) from 130 to 225 mm, whereas females from a mid-elevation stream matured at 90 to 170 mm (Kennedy et al. 2003). Based on age assignments, these mature females in the high-elevation stream were at least three years old and those in the mid-elevation stream were at least one year old. Longevity of brook trout in these two streams was also very different, with few fish older than age 4 found in the mid-elevation stream whereas many brook trout in the high-elevation stream were ten years old or older (up to 14 years). Growth was significantly slower in the high-elevation stream. Average lengths at age reported for brook trout in Montana of 76, 143, and 200 mm for ages 1 through 3, respectively, were similar or higher to lengths at age reported for New York and Michigan waters (Domrose 1963).

Brook trout spawn in the fall and their embryos incubate within the streambed through the winter until they emerge as fry during the spring (Greeley 1952; Lennon 1967; Blanchfield and Ridgway 1997: Holcombe et al. 2000; Zorn and Nuhfer 2007). Adult brook trout selected areas of groundwater influence for spawning (Curry and Noakes 1995).

Diets of brook trout consisted primarily of adult and immature macroinvertebrates, primarily insects (Allen and Claussen 1960; Allan 1981). Little to no evidence has been found of fish in stomachs of stream-resident brook trout (Allen and Claussen 1960; Allan 1981).

At landscape scales, brook trout preferred smaller streams with lower width-to-depth ratios and lower gradients at higher elevations (Josephson 1983; Chisholm and Hubert 1986; Kozel and Hubert 1989). At reach scales, brook trout preferred habitats that had pools and cover (Butler and Hawthorne 1968; Enk 1977; Josephson 1983; Riley et al. 1992). Pool volume (Riley et al. 1992) and the amount of overhead cover (Josephson 1983; Riley et al. 1992) have been identified as important for adult brook trout (Neumann and Wildman 2002). Shepard (2004) reported that brook trout reached higher densities than westslope cutthroat trout in a stream that had warmer temperatures, more woody debris, a higher proportion of fine sediment in the streambed, and a higher proportion of pool habitats compared to two other adjacent streams where westslope cutthroat trout dominated. Cunjak and Green (1984) found that brook trout dominated rainbow trout in slower-velocity water, indicating their preference for pools.

Age-0 brook trout occupied positions with velocities less than 20 cm/s and depths less than 40 cm at the microhabitat scale (Rose 1986). Age-1 and older brook trout preferred mean column velocities of 32 to 49 cm/s and depths from 20 to 60 cm (Baker and Coon 1997; Gunckel et al. 2002); age-0 brook trout used microhabitats with lower velocities and shallower depths (Baker and Coon 1997).

Nonnative Species Invasion and Establishment

Invasion by exotic species has led to major changes in native biological communities and has been implicated as a major cause of extinctions (Miller et al. 1989; D'Antonio and Vitousek 1992; Mooney and Cleland 2001) especially within freshwater ecosystems (Townsend 1996; Claudi and Leach 1999; Fuller et al. 1999; Kolar and Lodge 2001, 2002). Negative effects of non-native species are well documented; however, ecological outcomes of invasions can vary widely (Burger et al. 2001; Mooney and Cleland 2001; Dunham et al. 2002). Examples exist of invasive species altering the evolutionary pathway of native species by competitive exclusion, niche displacement, hybridization, introgression, predation, and ultimately extinction (Mooney and Cleland 2001).

Documented effects of exotic fish on native aquatic communities include reduction or extinction of native aquatic species, alteration of habitat, and introduction of parasites or disease organisms (Krueger and May 1991; Ross 1991; Vander Zanden et al. 1999; Taniguchi et al. 2002; Leyse et al. 2004; Vander Zanden et al. 2004). However, at least one study has shown no significant effects of exotic fish on native communities

(Wissinger et al. 2006). Competitive interactions between invasive and native species have generally been considered among the most important mechanisms driving invasion dynamics, but such interactions are often poorly understood (Byers 2000; Dunham et al. 2004).

Examination of ecological interactions during and following establishment of exotic species will provide insights into 1) how invasion affects communities (Bohn and Amundsen 2001), 2) how competitive exclusion might occur (Jaeger 1974), and 3) what managers might do to eliminate or reduce the risk of exotic invasion. Ontogenetic differences in species interactions might provide an opportunity to focus on life history stages where management actions might be most effective (Sakai et al. 2001; Taniguchi et al. 2002). Invasive species also offer excellent opportunities to study basic processes in population biology (Sakai et al. 2001). The importance of linking evolutionary and ecological consequences of anthropogenic changes to the environment, especially as it relates to species invasion and native species conservation, has been increasingly recognized, particularly in light of mounting evidence for much more rapid evolutionary responses than those previously considered (e.g., Taper and Case 1992 and reviews by Ashley et al. 2003 and Lambrinos 2004).

Niche, Competition, and Predation

Competition is the demand of more than one organism for the same resource of the environment in excess of the immediate supply (Darwin 1859). Niche has been variously defined (Grinnell 1917; Elton 1927; Hutchinson 1957; MacArthur and Levin

1967) and Leibold (1995) differentiates between environmental requirements and environmental effects of species. Hutchinson's (1957) definition of an "n-dimensional hypervolume" consisting of a volume within a multidimensional space whose axes are different biotic and abiotic conditions has gained popularity since its introduction. Hutchinson (1957) and Miller (1967) recognized a difference between the "fundamental niche," the range of abiotic and biotic conditions in which a species lives in the absence of other species (total potential), and the "realized niche," the actual niche a species occupies in the presence of another species (Jaeger 1974).

Freshwater environments offer comparatively few opportunities for specialization in fishes; consequently, most freshwater fishes have a wide tolerance of habitat types, flexibility in feeding habitats, and can share resources in their environment with several other species of fish (Larkin 1956). Flexible growth rates and high reproductive potential of freshwater fishes mitigate unfavorable periods of competition that may occur because of environmental factors and organization of freshwater fish communities is characterized by breadth at each level of the food chain rather than by a height of trophic levels in a pyramid (Larkin 1956). A review of 37 field studies on resource partitioning in fish assemblages from 1940 to 1983 concluded trophic separation was more important than habitat separation in fish assemblages, with 32% of the studies showing primary separation based on habitat, 57% based on food, and 11% based on time (Rose 1986).

Interference competition occurs when a dominant species or individual defends preferred resources and excludes subordinate species or individuals (Morse 1974, 1980; Jaeger 1974). Behavioral defense of a resource (i.e., territory) is necessary for interference competition to occur. Exploitation competition occurs when a species or individual is able to more efficiently use limited resources (i.e., food, shelter; Jaeger 1974; Davey et al. 2009). Exploitative competition occurs when organisms share a limited resource, whereas interference competition occurs when interactions of organisms reduces fitness of one or both organisms.

Defense of territories, or space, by salmonids probably evolved as a mechanism to make the most efficient use of the available food resources in lotic environments (Kalleberg 1958; Chapman 1966; Slaney and Northcote 1974; Rosenfeld and Taylor 2009). As food resources become more or less abundant, salmonids appear to adjust their defense of space by decreasing or increasing the size of their territories (Slaney and Northcote 1974; Dunbrack et al. 1996; Rosenfeld and Taylor 2009). Availability of slow velocity water in close proximity to faster velocity water is critically important for salmonids to minimize the energy necessary to maintain position, yet maximize the delivery of food items (Chapman 1966; Chapman and Bjornn 1969; Everest and Chapman 1972; Griffith 1972; Fausch and White 1981). Cutthroat trout typically exhibited a social hierarchical behavior in pools (e.g., Kalleberg 1958; Chapman 1966; Chapman and Bjornn 1969; Bachman 1984; Shepard et al. 1984; Nakano and Furukawa-Tanaka 1994; Gowan 2007), whereas brook trout typically exhibited territorial behavior (e.g., Newman 1956; Griffith 1972; Fausch and White 1981; Hakala and Hartman 2004; Zimmerman and Vondracek 2006; Buys et al. 2009).

Chapman (1966) suggested that stream salmonids compete for food and space through interference by choosing and defending positions, termed focal points. He believed competition for space has been substituted for competition for food among stream salmonids. He suggested that territory size is dependent upon food availability and regulates population density. Chapman and Bjornn (1969) further expanded and tested some of these theories, concluding that stream salmonids competed primarily for space as prime feeding positions that allowed individuals to most effectively feed on invertebrate drift.

Interspecific competition is often asymmetric, with individuals of one species reducing the fitness of individuals of the other species (Connell 1983; Lawton and Hassell 1981; Schoener 1983). Competitive exclusion occurs when one species eliminates another competing species because of a high degree of niche overlap (Jaeger 1974; Douglas et al. 1994). Jaeger (1974) suggested that a species might only exclude a competing species during periods when critical resources are scarce. He implied that it may be possible for an inferior species to ebb and flow in abundance as critical resources periodically become scarce and then abundant, as long as members of the inferior species either survive in small numbers or in a different location from which they can re-colonize after critical resources again become abundant. Taper and Case (1985) and Slatkin (1980) indicated that asymmetric competition would either lead to significant character displacement or to competitive exclusion.

Crowder (1990) suggested that the most rigorous evidence to demonstrate competitive interactions could be gained by showing “repeated changes in growth or abundance when resource levels or competitors are manipulated experimentally.” Peterson and Fausch (2003b) presented a conceptual framework for a manipulative field experiment to test for population-level mechanisms causing ecological effects and promoting invasion success by isolating segments of streams with different physical characteristics and physically removing the invasive species to document the response of the native species. They suggested that experiments of this type could provide 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.

Based on this literature review, I decided to investigate whether brook trout and westslope cutthroat trout occupied similar niches and if so, to attempt to infer what mechanisms might promote successful invasion by brook trout and allow them to displace westslope cutthroat trout. I conducted this research by removing brook trout from moderately long reaches of several headwater streams in the upper Missouri River basin of Montana and evaluating the response of westslope cutthroat trout populations during and following the removal of brook trout. I synthesize the results and suggest how these results can be applied in the conservation of native cutthroat trout populations throughout western North America.

Literature Cited

Adams, S. B. 1999. Mechanisms limiting a vertebrate invasion: brook trout in mountain streams of the northwestern USA. Doctoral dissertation, University of Montana, Missoula.

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2000. Movements of nonnative brook trout in relation to stream channel slope. Transactions of the American Fisheries Society 129:623-638.

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2001. Geography of invasion in mountain streams: consequences of headwater lake fish introductions. Ecosystems 4:296-307.

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2002. Changes in distribution of nonnative brook trout in an Idaho drainage over two decades. Transactions of the American Fisheries Society 131:561-568.

Allan, J. D. 1981. Determinants of diet of brook trout in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 38:184-192.

Allen, G. H., and L. G. Claussen. 1960. Selectivity of food by brook trout in a Wyoming beaver pond. Transactions of the American Fisheries Society 89:80-81.

Allendorf, F. W., and R. F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. Conservation Biology 2:170-184.

Angers, B., L. Bernatchez, A. Angers, and L. Desgroseillers. 1995. Specific microsatellite loci for brook charr reveal strong population subdivision on a microgeographic scale. Journal of Fish Biology 47:177-185.

Ashley, M. V., M. F. Willson, O. R. W. Pergams, D. J. O'Dowd, S. M. Gende, and J. S. Brown. 2003. Evolutionarily enlightened management. Biological Conservation 111:115-123.

Averett, R. C. 1962. Life history study of cutthroat trout in northern Idaho: studies of two races of cutthroat trout in northern Idaho. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project IDA-F-047-R-01, Boise.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113:1-32.

Baker, E. A., and T. G. Coon. 1997. Development and evaluation of alternative habitat suitability criteria for brook trout. Transactions of the American Fisheries Society 126:65-76.

Ball, O. P., and O. B. Cope. 1961. Mortality studies on cutthroat trout in Yellowstone Lake. Research Report 55, U.S. Department of Interior, Fish and Wildlife Service, Washington, D.C.

Behnke, R. J. 1979. Monograph of the native trouts of the genus *Salmo* of western North America. Final Report to USDI Bureau of Land Management and Fish and Wildlife Service, and USDA Forest Service, Region 2, Lakewood, Colorado.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Benjamin, J. R. 2006. Invasion by nonnative brook trout in Panther Creek, Idaho: roles of habitat quality, connectivity, and biotic resistance. Master's thesis. Boise State University, Boise, Idaho.

Benjamin, J. R., J. B. Dunham, and M. R. Dare. 2007. Invasion by nonnative brook trout in Panther Creek, Idaho: roles of local habitat quality, biotic resistance, and connectivity to source habitats. Transactions of the American Fisheries Society 136:875-888.

Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83-138 *in* W. R. Meehan, editor. Influences of forest and rangeland maangement on salmonid fishes and their habitats. American Fisheries Society Special Publication 19, Bethesda, Maryland.

Bjornn, T. C., and G. A. Liknes. 1986. Life history, status, and management of westslope cutthroat trout. Pages 57-96 *in* J. S. Griffith, editor. The ecology and management of interior stocks of cutthroat trout. Special Publication of the Western Division, American Fisheries Society, Bethesda, Maryland.

Blanchfield, P. J., and M. S. Ridgway. 1997. Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 54:747-756.

Bohn, T., and P. A. Amundsen. 2001. The competitive edge of an invading specialist. Ecology 82:2150-2163.

Bozek, M. A., and F. J. Rahel. 1991. Assessing habitat requirements of young Colorado River cutthroat trout by use of macrohabitat and microhabitat analyses. Transactions of the American Fisheries Society 120:571-581.

Brown, C. J. D. 1971. Fishes of Montana. Montana University Press, Bozeman.

Brown, R. S., and W. C. Mackay. 1995. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. Transactions of the American Fisheries Society 124:873-885.

Burger, J. C., M. A. Patten, T. R. Prentice, and R. A. Redak. 2001. Evidence for spider community resilience to invasion by non-native spiders. Biological Conservation 98:241-249.

Butler, R. L., and V. M. Hawthorne. 1968. The reactions of dominant trout to changes in overhead artificial cover. Transactions of the American Fisheries Society 97:37-41.

Buys, D. J., R. H. Hilderbrand, and J. L. Kershner. 2009. The effects of varied densities on the growth and emigration of adult cutthroat trout and brook trout in fenced stream enclosures. Western North American Naturalist 69:371-381.

Byers, J. E. 2000. Competition between two estuarine snails: implications for invasions of exotic species. Ecology 81:1225-1239.

Cegelski, C. C., M. R. Campbell, K. A. Meyer, and M. S. Powell. 2006. Multiscale genetic structure of Yellowstone cutthroat trout in the Upper Snake River Basin. Transactions of the American Fisheries Society 135:711-726.

Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. American Naturalist 100:345-357.

Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153-176 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams, Institute of Fisheries, University of British Columbia, Vancouver.

Chisholm, I. M., and W. A. Hubert. 1986. Influence of stream gradient on standing stock of brook trout in the Snowy Range, Wyoming. Northwest Science 60:137-139.

Claudi, R., and J. H. Leach. 2000. Nonindigenous freshwater organisms: vectors, biology and impacts. Lewis Publishers, London.

Coleman, M. A., and K. D. Fausch. 2007. Bottleneck in age-0 Colorado River cutthroat trout reared in laboratory streams. Transactions of the American Fisheries Society 136:639-654.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist 122:661-696.

Crowder, L. B. 1990. Community ecology. Pages 609-632 *in* C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Cunjak, R. A., and J. M. Green. 1984. Species dominance by brook trout and rainbow trout in a simulated stream environment. Transactions of the American Fisheries Society 113:737-743.

Curry, R. A., and D. L. G. Noakes. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 52:1733-1740.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. Annual Review of Ecology and Systematics 23:63-87.

Darwin, C. 1859. On the origin of species. John Murray. London.

Davey, A. J. H., C. P. Doncaster, and O. D. Jones. 2009. Distinguishing between interference and exploitation competition for shelter in a mobile fish population. Environmental Modeling and Assessment 14:555-562.

de la Hoz Franco, E. A. D., and P. Budy. 2005. Effects of biotic and abiotic factors on the distribution of trout and salmon along a longitudinal stream gradient. Environmental Biology of Fishes 72:379-391

.

DeRito, J. N. 2004. Assessment of reproductive isolation between Yellowstone cutthroat trout and rainbow trout in the Yellowstone River, Montana. Master's thesis. Montana State University, Bozeman.

Domrose, R. J. 1963. Age and growth of brook trout, *Salvelinus fontinalis*, in Montana. Proceedings of the Montana Academy of Sciences 23:47-62.

Douglas, M. E., P. C. Marsh, and W. L. Minckley. 1994. Indigenous fishes of western North America and the hypothesis of competitive displacement: *Meda fulgida* (Cyprinidae) as a case study. Copeia 1994:9-19.

Downs, C. C., R. G. White, and B. B. Shepard. 1997. Age at sexual maturity, sex ratio, fecundity, and longevity of isolated headwater populations of westslope cutthroat trout. North American Journal of Fisheries Management 17:85-92.

Dunbrack, R. L., L. Clarke, and C. Bassler. 1996. Population level differences in aggressiveness and their relationship to food density in a stream salmonid (*Salvelinus fontinalis*). Journal of Fish Biology 48:615-622.

Dunham, J. B., S. B. Adams, R. E. Schroeter, and D. C. Novinger. 2002. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. Reviews in Fish Biology and Fisheries 12:373–391.

Dunham, J., B. Rieman, and G. Chandler. 2003. Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. North American Journal of Fisheries Management 23:894-904.

Dunham, J. B., D. S. Pilliod, and M. K. Young. 2004. Assessing the consequences of nonnative trout in headwater ecosystems in western North America. Fisheries 29(6):18-26.

Elton, C. 1927. Animal ecology. Sidgwick and Jackson, London.

Enk, M. D. 1977. Instream overhead bank cover and abundance in two Michigan streams. Master's thesis. Michigan State University, East Lansing.

Erman, D. C. 1986. Long-term structure of fish populations in Sagehen Creek, California. Transactions of the American Fisheries Society 115:682-692.

Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 29:91-100.

Fausch, K. D. 1989. Do gradient and temperature affect distribution of, and interactions between juvenile brook char and other salmonids in streams? Physiology and Ecology of Japan, Special Volume 1:303–322.

Fausch, K. D., and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220-1227.

Fleener, G. G. 1951. Life history of the cutthroat trout, *Salmo clarki* Richardson, in Logan River, Utah. Transactions of the American Fisheries Society 81:235-248.

Flick, W. A., and D. A. Webster. 1975. Movement, growth, and survival in a stream population of wild brook trout (*Salvelinus fontinalis*) during a period of removal of non-trout species. Journal of the Fisheries Research Board of Canada 32:1359-1367.

Fuller, P. L., L. G. Nico, and J. D. Williams. 1999. Nonindigenous fishes introduced into inland waters of the United States. American Fisheries Society Special Publication 27, Bethesda, Maryland.

Gowan, C. 2007. Short-term cues used by foraging trout in a California stream. Environmental Biology of Fishes 78:317-331.

Gowan, C., and K. D. Fausch. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370-1381.

Greeley, J. R. 1952. The spawning habits of brook, brown and rainbow trout, and the problem of egg predators. Transactions of the American Fisheries Society 62:239-247.

Gresswell, R. E. 1988. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.

Gresswell, R. E. 1995. Yellowstone cutthroat trout. Pages 36-54 *in* M. K. Young, technical editor. Conservation assessment for inland cutthroat trout, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Gresswell, R. E., W. J. Liss, G. L. Larson, and P. J. Bartlein. 1997. Influence of basin-scale physical variables on life history characteristics of cutthroat trout in Yellowstone Lake. North American Journal of Fisheries Management 17:1046-1064.

Griffith, J. S., Jr. 1970. Interaction of brook trout and cutthroat trout in small streams. Doctoral dissertation. University of Idaho, Moscow.

Griffith, J. S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada 29:265-273.

Griffith, J. S., Jr. 1988. Review of competition between cutthroat trout and other salmonids. American Fisheries Society Symposium 4:134-140.

Grinnell, J. 1917. The niche-relationships of the California Thrasher. Auk 34:427-433.

Gunckel, S. L., A. R. Hemmingsen, and J. L. Li. 2002. Effect of bull trout and brook trout interactions on foraging habitat, feeding behavior, and growth. Transactions of the American Fisheries Society 131:1119-1130.

Hadley, K. 1984. Status report on the Yellowstone cutthroat trout (*Salmo clarki bouvieri*) in Montana. Final Report of K. Hadley to Montana, Department of Fish, Wildlife and Parks, Helena.

Hakala, J. P., and K. J. Hartman. 2004. Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. Hydrobiologia 515:203-213.

Hanzel, D. A. 1959. The distribution of the cutthroat trout (*Salmo clarki*) in Montana. Proceedings of the Montana Academy of Sciences 19:32-71.

Harig, A. L., K. D. Fausch, and M. K. Young. 2000. Factors influencing success of greenback cutthroat trout translocations. North American Journal of Fisheries Management 20:994-1004.

Heggenes, J., T. G. Northcote, and A. Peter. 1991. Seasonal habitat selection and preferences by cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 48:1364-1370.

Hepworth, D. K., M. J. Ottenbacher, and C. B. Chamberlain. 2002. A review of a quarter century of native trout conservation in southern Utah. Intermountain Journal of Sciences 8:125-142.

Hilderbrand, R. H., and J. L. Kershner. 2000. Conserving inland cutthroat trout in small streams: how much stream is enough? North American Journal of Fisheries Management 20:513-520.

Hoelscher, B., and T. C. Bjornn. 1989. Habitat, densities, and potential production of trout and char in Pend Oreille Lake tributaries. Federal Aid in Fish Restoration Job Completion Report, Project F-71-R-10, Subproject III, Job 8, Idaho Department of Fish and Game, Boise.

Holcombe, G. W., M. S. Pasha, K. M. Jensen, J. E. Tietge, and G. T. Ankley. 2000. Effects of photoperiod manipulation on brook trout reproductive development, fecundity, and circulating sex steroid concentrations. North American Journal of Aquaculture 62:1-11.

Hutchinson, G. E. 1957. Concluding remarks - Population studies: animal ecology and demography. Cold Springs Harbor Symposium on Quantitative Biology 22:415-427.

Ireland, S. C. 1993. Seasonal distribution and habitat use of westslope cutthroat trout in a sediment-rich basin in Montana. Master's thesis. Montana State University, Bozeman.

Irving, R. B. 1954. Ecology of the cutthroat trout in Henrys Lake, Idaho. Transactions of the American Fisheries Society 84:275-296.

Jaeger, R. G. 1974. Competitive exclusion - comments on survival and extinction of species. Bioscience 24:33-39.

Johnson, H. E. 1963. Observations on the life history and movement of cutthroat trout, *Salmo clarki*, in Flathead River drainage, Montana. Proceedings of the Montana Academy of Sciences 23: 96-110.

Josephson, D. C. 1983. Environmental factors related to the abundance and distribution of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) and seasonal movements of brown trout in selected Virginia watersheds. Master's thesis. Virginia Polytechnic Instititute and State University, Blacksburg.

Kaeding, L. R., and G. D. Boltz. 2001. Spatial and temporal relations between fluvial and allacustrine Yellowstone cutthroat trout, *Oncorhynchus clarki bouvieri*, spawning in the Yellowstone River, outlet stream of Yellowstone Lake. Environmental Biology of Fishes 61:395-406.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L., and *S. trutta* L.). Institute of Freshwater Research Drottningholm 39:55-98.

Kennedy, B. M., D. P. Peterson, and K. D. Fausch. 2003. Different life histories of brook trout populations invading mid-elevation and high-elevation cutthroat trout streams in Colorado. Western North American Naturalist 63:215-223.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16:199-204.

Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. Science 298:1233-1236.

Kondratieff, M. C. 2004. Evaluating brook trout jumping performance using adjustable waterfalls. Master's thesis. Colorado State University, Fort Collins.

Kondratieff, M. C., and C. A. Myrick. 2006. How high can brook trout jump? A laboratory evaluation of brook trout jumping performance. Transactions of the American Fisheries Society 135:361-370.

Kozel, S. J. and W. A. Hubert. 1987. Age estimates of brook trout from high-elevation Rocky Mountain streams using scales and otoliths. Northwest Science 61:216-219.

Krueger, C. C., and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48:66-77.

Kruse, C. G., W. A. Hubert, and F. J. Rahel. 2000. Status of Yellowstone cutthroat trout in Wyoming waters. North American Journal of Fisheries Management 20:693-705.

Lambrinos, J. G. 2004. How interactions between ecology and evolution influence contemporary invasion dynamics. Ecology 85:2061-2070.

Larkin, P. A. 1956. Interspecific competition and population control in freshwater fish. Journal of the Fisheries Research Board of Canada 13:327-342.

Larson, G. L., and S. E. Moore. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachian Mountains. Transactions of the American Fisheries Society 114:195-203.

Lawton, J. H., and M. P. Hassell. 1981. Asymmetrical competition in insects. Nature 289:793-795.

Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. Ecology 76:1371-1382.

Lennon, R. E. 1967. Brook trout of Great Smoky Mountains National Park. United States Bureau of Sport Fish and Wildlife Technical Paper 15:1-18.

Leyse, K. E., S. P. Lawler, and T. Strange. 2004. Effects of an alien fish, *Gambusia affinis*, on an endemic California fairy shrimp, *Linderiella occidentalis*: implications for conservation of diversity in fishless waters. Biological Conservation 118:57-65.

Liknes, G. A., and P. J. Graham. 1988. Westslope cutthroat trout in Montana: life history, status, and management. American Fisheries Society Symposium 4:53-60.

Lukens, J. R. 1978. Abundance, movements and age structure of adfluvial westslope cutthroat trout in the Wolf Lodge Creek drainage, Idaho. Master's thesis, University of Idaho, Moscow.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101:377-385.

MacCrimmon, H. R., and J. S. Campbell. 1969. World distribution of brook trout, *Salvelinus fontinalis*. Journal of the Fisheries Research Board of Canada 26:1699-1725.

MacPhee, C. 1966. Influence of differential angling mortality and stream gradient on fish abundance in a trout-sculpin biotope. Transactions of the American Fisheries Society 95:381-387.

Magnan, P., R. Proulx, and M. Plante. 2005. Integrating the effects of fish exploitation and interspecific competition into current life history theories: an example with lacustrine brook trout (*Salvelinus fontinalis*) populations. Canadian Journal of Fisheries and Aquatic Sciences 62:747-757.

May, B. E., W. Urie, and B. B. Shepard. 2003. Range-wide status of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*): 2001. U.S. Department of Agriculture, Gallatin National Forest, Bozeman, Montana.

May, B. E., S. E. Albeke, and T. Horton. 2007. Range-wide status assessment for Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*): 2006. Yellowstone Cutthroat Trout Interagency Coordination Group Report to Montana Department of Fish, Wildlife and Parks, Helena.

McHugh, P., and P. Budy. 2005. An experimental evaluation of competitive and thermal effects on brown trout (*Salmo trutta*) and Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) performance along an altitudinal gradient. Canadian Journal of Fisheries and Aquatic Sciences 62:2784-2795.

McIntyre, J. D., and B. E. Rieman. 1995. Westslope cutthroat trout. Pages 1-15 *in* M. K. Young, technical editor. Conservation assessment for inland cutthroat trout. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

McMahon, T. E., A. V. Zale, F. T. Barrows, J. H. Selong, and R. J. Danehy. 2007. Temperature and competition between bull trout and brook trout: a test of the elevation refuge hypothesis. Transactions of the American Fisheries Society 136:1313-1326.

Meyer, K. A., D. J. Schill, J. A. Lamansky, M. R. Campbell, and C. C. Kozfkay. 2006. Status of Yellowstone cutthroat trout in Idaho. Transactions of the American Fisheries Society 135:1329-1347.

Meyer, K. A., D. J. Schill, F. S. Elle, and J. A. Lamansky. 2003. Reproductive demographics and factors that influence length at sexual maturity of Yellowstone cutthroat trout in Idaho. Transactions of the American Fisheries Society 132:183-195.

Miller, R. B. 1953. Comparative survival of wild and hatchery-reared cutthroat trout in a stream. Transactions of the American Fisheries Society 83:120-130.

Miller, R.S. 1967. Pattern and process in competition. Pages 1-74 *in* J. Cragg, editor. Advances in ecological research, Volume 4. Academic Press, New York.

Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fishes during the past century. Fisheries 14(6):22-38.

Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences of the United States of America 98:5446-5451.

Moore, K. M. S., and S. V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences 45:1921-1930.

Morse, D.H. 1974. Niche breadth as a function of social dominance. American Naturalist 108:818-830.

Morse, D.H. 1980. Behavioral mechanisms in ecology. Harvard University Press, Cambridge.

Nakano, S., K. D. Fausch, and T. Furukawa-Tanaka. 1992. Resource utilization by bull char and cutthroat trout in a mountain stream in Montana, USA. Japanese Journal of Ichthyology 39:211-216.

Neumann, R. M. and T. L. Wildman. 2002. Relationships between trout habitat use and woody debris in two Southern New England streams. Ecology of Freshwater Fish 11:240-250.

Newman M. A. 1956. Social behavior and interspecific competition in two trout species. Physiological Zoology 29:64-81.

Novinger, D. C., and F. J. Rahel. 2003. Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. Conservation Biology 17:772-781.

Paul, A. J., and J. R. Post. 2001. Spatial distribution of native and nonnative salmonids in streams of the eastern slopes of the Canadian Rocky Mountains. Transactions of the American Fisheries Society 130:417-430.

Peters, D. 1988. Third-year evaluation of sediment and fish populations in selected tributaries in Rock Creek and the Bitterroot River drainage. Montana Department of Fish, Wildlife and Parks, Missoula.

Peterson, D. P., B. E. Rieman, J. B. Dunham, K. D. Fausch, and M. K. Young. 2008. Analysis of trade-offs between threats of invasion by nonnative brook trout (*Salvelinus fontinalis*) and intentional isolation for native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). Canadian Journal of Fisheries and Aquatic Sciences 65: 557-573.

Peterson, D. P., and K. D. Fausch. 2003a. Upstream movement by nonnative brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Oncorhynchus clarki*) habitat. Canadian Journal of Fisheries and Aquatic Sciences 60:1502-1516.

Peterson, D. P., and K. D. Fausch. 2003b. Testing population-level mechanisms of invasion by a mobile vertebrate: a simple conceptual framework for salmonids in streams. Biological Invasions 5:239-259.

Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of brook trout on native cutthroat trout. Ecological Applications 14:754-772.

Petty, J. T., P. J. Lamothe, and P. M. Mazik. 2005. Spatial and seasonal dynamics of brook trout populations inhabiting a central Appalachian watershed. Transactions of the American Fisheries Society 134:572-587.

Power, G. 2002. Charrs, glaciations and seasonal ice. Environmental Biology of Fishes 64:17-35.

Pratt, K. L. 1984. Habitat use and species interactions of juvenile cutthroat (*Salmo clarki lewisi*) and bull trout (*Salvelinus confluentus*) in the upper Flathead River basin. Master's thesis. University of Idaho, Moscow.

Propst, D. L., J. A. Stefferud, and P. R. Turner. 1992. Conservation and status of Gila trout, *Oncorhynchus gilae*. The Southwestern Naturalist 37:117-125.

Rieman, B. E., and K. Apperson. 1989. Status and analysis of salmonid fisheries: westslope cutthroat trout synopsis and analysis of fishery information. Federal Aid in Fish Restoration, Project F-73-R-11, Subproject II, Job 1, Idaho Department of Fish and Game, Boise.

Riley, S. C., K. D. Fausch, and C. Gowan. 1992. Movement of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. Ecology of Freshwater Fish 1:112-122.

Rodriguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83:1-13.

Roghair, C. N. 2005. Brook trout movement during and after recolonization of a naturally defaunated stream reach. North American Journal of Fisheries Management 25:777-784.

Rose, G. A. 1986. Growth decline in subyearling brook trout (*Salvelinus fontinalis*) after emergence of rainbow trout (*Salmo gairdneri*). Canadian Journal of Fisheries and Aquatic Sciences 43:187-193.

Rosenfeld, J. S. and J. Taylor. 2009. Prey abundance, channel structure and the allometry of growth rate potential for juvenile trout. Fisheries Management and Ecology 16:202-218.

Ross, S. T. 1991. Mechanisms structuring stream fish assemblages - are there lessons from introduced species? Environmental Biology of Fishes 30:359-368.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32:305-332.

Schmetterling, D. A. 2001. Seasonal movements of fluvial westslope cutthroat trout in the Blackfoot River drainage, Montana. North American Journal of Fisheries Management 21:507-520.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122:240-285.

Shepard, B. B. 1983. Evaluation of a combined methodology for estimating fish abundance and lotic habitat in mountain streams of Idaho. Master’s thesis. University of Idaho, Moscow.

Shepard, B. B. 2004. Factors that may be influencing nonnative brook trout invasion and their displacement of native westslope cutthroat trout in three adjacent southwestern Montana streams. North American Journal of Fisheries Management 24:1088-1100.

Shepard, B. B., B. Sanborn, L. Ulmer, and D. C. Lee. 1997. Status and risk of extinction for westslope cutthroat trout in the upper Missouri River Basin, Montana. North American Journal of Fisheries Management 17:1158-1172.

Shepard, B. B., B. E. May, and W. Urie. 2005. Status and conservation of westslope cutthroat trout within the western United States. North American Journal of Fisheries Management 25:1426-1440.

Shepard, B. B., K. L. Pratt, and P. J. Graham. 1984. Life histories of westslope cutthroat and bull trout in the upper Flathead River Basin, Montana. Report of Montana Department of Fish, Wildlife and Parks to U.S. Environmental Protection Agency, Contract Number R008224-01-5, Helena.

Slaney, P. A., and T. G. Northcote. 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. Journal of the Fisheries Research Board of Canada 31:1201-1209.

.

Slatkin, M. 1980. Ecological character displacement. Ecology 61:163-177.

Smith, M. W., and J. W. Saunders. 1958. Movements of brook trout, *Salvelinus fontinalis* (Mitchill), between and within fresh and salt water. Journal of the Fisheries Research Board of Canada 15:1403-1449.

Smith, C. E., W. P. Dwyer, and R. G. Piper. 1983. Effect of water temperature on egg quality of cutthroat trout. Progressive Fish Culturist 45:176-178

Taniguchi, Y., K. D. Fausch, and S. Nakano. 2002. Size-structured interactions between native and introduced species: can intraguild predation facilitate invasion by stream salmonids? Biological Invasions 4:223-233.

Taper, M. L., and T. J. Case. 1992. Models of character displacement and the theoretical robustness of taxon cycles. Evolution 46:317-333.

Taylor, E. B., M. D. Stamford, and J. S. Baxter. 2003. Population subdivision in westslope cutthroat trout (*Oncorhynchus clarki lewisi*) at the northern periphery of its range: evolutionary inferences and conservation implications. Molecular Ecology 12:2609-2622.

Thurow, R. F., and T. C. Bjornn. 1978. Response of cutthroat trout populations to the cessation of fishing in St. Joe River tributaries. Federal Aid to Fish and Wildlife Restoration Project F-60-R, Idaho Department of Fish and Game, Boise.

Townsend, C. R. 1996. Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. Biological Conservation 78:13-22.

Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401:464-467.

Vander Zanden, M. J., J. D. Olden, J. H. Thorne, and N. E. Mandrak. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. Ecological Applications 14:132-148.

Van Eimeren, P. 1996. Westslope cutthroat trout *Oncorhynchus clarki lewisi*. Pages 1-10 *in* D. A. Duff, editor. Conservation assessment for inland cutthroat trout: distribution, status, and habitat management implications. U.S. Department of Agriculture, Forest Service, Intermountain Region, Ogden, Utah.

Varley, J. D., and R. E. Gresswell. 1988. Ecology, status, and management of the Yellowstone cutthroat trout. American Fisheries Society Symposium 4:13-24.

Wissinger, S. A., A. R. Mcintosh, and H. S. Greig. 2006. Impacts of introduced brown and rainbow trout on benthic invertebrate communities in shallow New Zealand lakes. Freshwater Biology 51:2009-2028.

Wofford, J. E. B., R. E. Gresswell, and M. A. Banks. 2005. Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. Ecological Applications 15:628-637.

Wydoski, R. S. 2003. Fecundity and recruitment potential of coastal cutthroat trout in Oregon and Washington. California Fish and Game 89:107-127.

Wydoski, R. S., and E. L. Cooper. 1966. Maturation and fecundity of brook trout (*Salvelinus fontinalis*) from infertile streams. Journal of the Fisheries Research Board of Canada 23:623-649.

Young, M. K. 1998. Absence of autumnal changes in habitat use and location of adult Colorado River cutthroat trout in a small stream. Transactions of the American Fisheries Society 127:147-151.

Zimmerman, J. K. H., and B. Vondracek. 2006. Effects of stream enclosures on drifting invertebrates and fish growth. Journal of the North American Benthological Society 25:453-464.

Zorn, T. G., and A. J. Nuhfer. 2007. Regional synchrony of brown trout and brook trout population dynamics among Michigan rivers. Transactions of the American Fisheries Society 136:706-717.

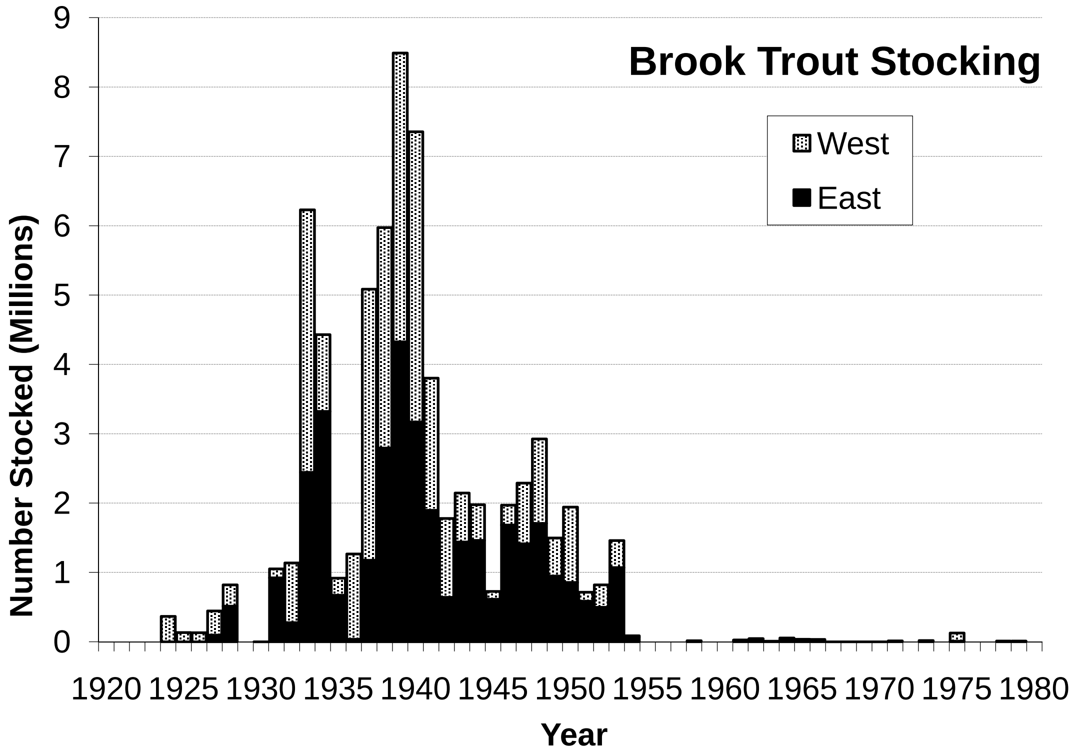

Figure 1.1. Number of brook trout stocked by Montana Fish, Wildlife and Parks into streams and rivers east and west of the Continental Divide within the historical range of westslope cutthroat trout.

CHAPTER 2

INVESTIGATION INTO BIAS AND VARIABILITY IN ESTIMATES OF POPULATION SIZE AND BIOMASS WHEN CATCHES OF INDIVIDUALS ARE LARGE RELATIVE TO THE TOTAL POPULATION

Abstract

Biomass of a fish population has traditionally been estimated by multiplying the mean weight of captured fish by the estimated number of fish, with its variance estimated as the product of two variances (hereafter OLD method). I present and evaluate methods for estimating fish biomass in small streams (< 5 m wetted width) that use a finite population correction factor (FPC) in conjunction with removal population estimators under an assumption of a constant capture probability. FPC estimators I investigated to better estimate the variance of biomass estimates were an *a priori* sample design estimator (hereafter FPCL; Lohr 1999) and an *a posteriori* modeled estimator (hereafter FPCM). Both methods take advantage of the fact that a relatively high proportion of the total population is normally captured and can be weighed during removal estimates. I also incorporated biomass estimates for fish that were captured and measured (mm; TL), but not weighed, using length-weight regression predictions ($FPCM_{reg}$). Variances computed using the FPCL and FPCM methods were nearly identical when all captured fish were weighed indicating that the FPCM method can be used to partition the estimates of variance. Discrepancies between the two methods were because the FPCM method incorporated measurement error and the FPCL method did not. The FPCL and FPCM methods had significantly smaller CVs and root-MSEs than the OLD method for field

(CVs) and simulated (CVs and root-MSEs) data. Coverage by 95% CIs for the FPCL and FPCM methods were much closer to the 95% nominal level than for the OLD method, especially when capture probabilities were higher than 0.5. For 619 field-derived biomass estimates where all captured fish were weighed, the median CVs for the FPCL (0.048) and FPCM (0.049) methods were significantly lower (Wilcoxon sign-ranked test; $P < 0.001$) than the OLD method, but not significantly different from each other. When various portions of captured fish were not weighed but estimated using length-weight regression relationships, the $FPCM_{reg}$ method had significantly lower CVs (median = 0.043) than both the FPCL and OLD method (medians for both = 0.817; Wilcoxon sign-ranked test; $P < 0.001$, n=96). Using simulated data I found that removal population estimates can deviate significantly from true population sizes, especially when the ratio of the number of captured fish to the number estimated is less than 0.6. These deviations clustered nearer to zero when the ratio of captured fish to the estimated number was 0.7 or higher.

Introduction

Estimating fish abundance or biomass is important for monitoring fish management activities (e.g., Ricker 1975; Hatch et al. 1981; Lewis et al. 1987; Smith and Gavaris 1993; Krause et al. 2002). Biomass, or standing crop, estimates are often made to evaluate production of fish populations and fisheries (e.g., Newman and Martin 1983; Quinn and Deriso 1999). Estimation of biomass is often preferred over other measures because it is not as sensitive to changes in population size structure. A problem with the estimator currently used to estimate biomass is that estimates of variation associated with these biomass estimates are usually large, making it difficult to determine if statistically significant changes have occurred (Dauwalter et al. 2009). Consequently, any estimator that provides a better estimate of the variation in biomass estimates (i.e., lower variance) will provide a better method for detecting statistically significant changes.

The traditional method (hereafter OLD method) for estimating biomass (Hayes et al. 2007) computes biomass by multiplying the population estimate by the mean weight of captured fish. The variance in both the population estimate and mean weight estimate are used to estimate the variance of the biomass estimate using the product of two variances. Newman and Martin (1983) presented methods to compute biomass estimates and illustrated how to reduce variance of these estimates by summing proportional estimates of biomass over relatively narrow size, or age, groups.

Depletion or removal population estimators (Leslie and Davis 1939; DeLury 1947; Ricker 1975; Zippin 1958; White et al. 1982) are often used to estimate populations, particularly of trout in streams (e.g., Peterson et al. 2004; Rosenberger and Dunham 2005). Removal estimators have been shown to be biased, especially when only two removal efforts are made and capture probabilities are less than 0.8 (Mahon 1980; White et al. 1982; Riley and Fausch 1992; Peterson et al. 2004). Capture probabilities estimated from removal estimators are often over-estimated causing under-estimates of the population (Mahon 1980; Peterson et al. 2004; Rosenberger and Dunham 2005). As reported by Rosenberger and Dunham (2005), capture probabilities can be influenced by the size of the stream (Bayley and Dowling 1993; Kruse et al. 1998; Peterson et al. 2004), complexity of the habitat (Rodgers et al. 1992; Kruse et al. 1998; Mullner et al. 1998), fish species and size (Büttiker 1992; Bayley and Dowling 1993; Dolan and Miranda 2003), density of fish (Kruse et al. 1998), and level of effort (Riley and Fausch 1992; Riley et al. 1993; Peterson et al. 2004). Capture probabilities generally decline with subsequent removal efforts and larger fish generally have higher capture probabilities than smaller fish. Most researchers try to minimize size-effects by making separate estimates for fish of similar sizes, or by excluding smaller individuals. Mesa and Schreck (1989) indicated that behavioral or physiological responses to an electric field during sampling may also influence capture probabilities, but observed little change in the behavior of cutthroat trout exposed to repeated electrofishing removals in the field.

Mahon (1980) estimated biomass using removal estimators (Leslie and Davis 1939; DeLury 1947) of total weight of fish caught during each removal effort and by the OLD method. He concluded that estimating biomass using the OLD method was preferred because it was simpler to estimate and estimates using these two methods were not significantly different. The OLD method of computing biomass has often been used to estimate biomass of trout in small streams in conjunction with some type of removal population estimator (e.g., Scarnecchia et al. 1987; Jones et al. 2003).

I present two additional methods for estimating biomass that use a finite population correction factor (FPC) to take advantage of the fact that relatively high proportions of the total population are normally captured and can be weighed during removal estimates conducted in small streams (< 5 m wetted width). One of these FPC methods uses the sample design *a priori* approach of Lohr (1999), whereas the other is a model-based approach (Royall 1970; Valiant et al. 2000) that allows for partitioning of the variance components. Estimates of biomass using these three estimators are identical, but estimates of variance among these methods differ. Performance of these three estimators was evaluated by comparing magnitudes of coefficients of variation for both field and simulated data, and coverages of estimated 95% confidence intervals and magnitudes of root of mean squared errors for simulated data.

Methods

I estimate biomass and its associated variance using the OLD and FPC estimators. I first present these estimators and then apply these estimators to simulated and field data to evaluate their performance. Because removal population estimates and their associated variances are used to estimate biomass, the bias of population estimates computed using the maximum likelihood removal estimator of Otis et al. (1978:108), originally recommended by Zippin (1958), is also evaluated. This removal estimator assumes a constant probability of capture among individuals and removal efforts. For this simulation analysis I only explore the bias of the removal estimator under an assumption of constant capture. I later discuss the implications of the assumption of constant capture probabilities and application of the removal estimator to field estimates.

Traditional (OLD) Method

The traditional formula for estimating biomass (Hayes et al. 2007) is: $\widehat{W} = \widehat{N} * \overline{w}$, where $\widehat{W}$ is the estimated biomass, $\widehat{N}$ is the population estimate, and $\overline{w}$ is the mean weight of the captured fish. I estimate variance by $\widehat{V}(\widehat{W}) = \widehat{N}^2 * \widehat{V}(w) + \overline{w}^2 * \widehat{\mathrm{V}}(\widehat{\mathrm{N}}) + \widehat{V}(\widehat{N}) * \widehat{V}(w)$, based on the product of two independent estimates, where $\widehat{V}$ indicates variance estimates. My variance formula differs from that of Hayes et al. (2007) because I added the cross-product of the two variances (last term in above equation), rather than subtract this cross-product as Hayes et al. (2007) did. Hayes et al. (2007) cited Goodman (1960) for their formulation of the variance estimator for an unbiased estimate of variance. This variance estimator assumes that estimates of population number and mean weight are independent, a condition that Hayes et al. (2007) and I deemed reasonable; however, Goodman (1960:710) suggested this formula was only appropriate if the estimates of both population number ($\widehat{N}$) and mean weight ($\overline{w}$) are unbiased. Estimates of population number using removal estimators have been shown to be biased (e.g., White et al. 1982; Peterson et al. 2004; Rosenberger and Dunham 2005). Goodman (1960) suggested adding the cross-product of the two variances if either of the estimates is biased.

To compute confidence intervals, Hayes et al. (2007) recommended applying a lognormal distribution and I concur with their recommendation; however, the equation they provided appeared to be in error. I compute 95% confidence intervals (95% CIs) using the formula: $e^{(\mu \pm 1.96\sqrt{\gamma})}$, where μ and γ are estimated using estimates of the expected values for biomass and variance of the biomass: $\mu = \log_n(\widehat{W}) - \frac{1}{2}\log_n\left(1 + \frac{V(\widehat{W})}{(\widehat{W})^2}\right)$ and $\gamma = \log_n\left(1 + \frac{V(\widehat{W})}{(\widehat{W})^2}\right)$.

Finite Population Correction (FPC) Methods

I use two different methods for applying a finite population correction factor to estimate biomass and its variance. The first method follows the recommendation of Lohr (1999) that uses a sample design, *a priori*, approach (hereafter designated FPCL). In this approach biomass is estimated using the same formula as the OLD method; however, variance is approximated by $\hat{V}(\widehat{W}) = \left[\widehat{N}^2 * \left(1 - \frac{n}{\widehat{N}}\right) * \frac{\hat{V}(w)}{n}\right] + \left[\overline{w}^2 * \hat{V}(\widehat{N})\right] + \left(1 - \frac{n}{\widehat{N}}\right) * \frac{\hat{V}(w)}{n} * \hat{V}(\widehat{N})$.

The second method is a model-based, *a posteriori*, method (hereafter designated FPCM) based on estimating totals of finite populations using models (Royall 1970; Valiant et al. 2000). The primary advantage of this model-based method for this project is that it allows for the partitioning of estimates of weights and their associated variances. The FPCM method estimates biomass by summing weights of all fish that are captured and weighed with predicted weights of non-captured fish (estimated number minus the number of captured fish) as $\widehat{W}_{\text{tot}} = W_{\text{weighed}} + \widehat{W}_{\text{non-captured}}$, where $\widehat{W}_{\text{tot}}$ is the total estimated weight, W_{weighed} is the sum of the weights of all weighed fish, and $\widehat{W}_{\text{non-captured}}$ is the predicted weight of fish not captured. Thus, weights of captured fish represent "true" weights for this portion of the sampled population and I need to predict the total weight and variance for the non-captured portion of the population.

To estimate the total weight of non-captured fish I applied a randomly stopped sums estimator (Chow et al. 1965), where the number of non-captured fish is a random variable. The total weight ($W_{non\text{-}captured}$) of non-captured fish is: $W_{non-captured} = \sum_{i=1}^{U} x_i$, where x_i is the weight of the i^{th} non-captured fish and U is the number of non-captured fish. This is called a randomly stopped sum because the termination index for the sum is itself a random variable. Thus, I need to find the expectation and variance for $W_{non\text{-}captured}$. Because the means and variances of both the weights of individual non-captured fish (x) and the number of non-captured fish (U) are finite, these expectations are $E(W_{non\text{-}captured}) = M_{non\text{-}captured} * M_x$ and $V(W_{non\text{-}captured}) = V_X * M_{non\text{-}captured} + M_X^2 * V_{non\text{-}captured}$, where $M_{non\text{-}captured}$ is the expected number of non-captured fish, M_x is the mean weight of non-captured fish, $V_{non\text{-}captured}$ is the variance in the number of the non-captured fish, and V_x is the variance in the weight of non-captured fish (Chow et al. 1965). I use estimates of mean weight and its variance for captured fish to estimate these values for non-captured fish, and the estimated population number minus the number captured and weighed to estimate the number of non-captured fish. Consequently, biomass of all non-captured fish (estimated number minus number captured) is estimated by $\widehat{W}_{non-captured} = (\widehat{N} - n) * \overline{w}$. The variance of the non-captured portion is estimated as:

$\hat{V}(\widehat{W}_{non-captured}) = [(\widehat{N} - n) * \hat{V}_n(w)] + [\overline{w}^2 * \hat{V}(\widehat{N})] + \left[(\widehat{N} - n)^2 * \frac{\hat{V}(w)}{n}\right]$, with the final term representing the uncertainty in the estimate of the mean.

I incorporate measurement errors for the weighed fish by assuming these measured weights follow a uniform distribution related to scale accuracy in a field setting. I have assumed a field and scale accuracy of 0.5 g on either side of recorded weights (range 1.0 g). Scale accuracy for electronic scales that I used in the field (O'Haus ®) was rated at 0.1 g, but I rounded weights to the nearest gram and assumed that scale accuracy caused by field conditions (i.e., water on fish) was 0.5 g. Gutreuter and Krzoska (1994) reported that coefficients of variation for in situ weights of common carp *Cyprinus carpio*, bluegills *Lepomis macrochirus*, and black crappies *Pomoxis nigromaculatus* were much higher than for length measurements, but they used a 1,000-g spring scale (accuracy of 1.0 g) to weigh the bluegills and black crappies and a 20-kg spring scale (accuracy of 0.05 kg) to weigh the carp.

Variance estimates with a uniform distribution range of 1.0 g translates to estimated variances of 1/12, or 0.0833, based on the uniform variance formula $Var = \left[\frac{(a-b)^2}{12}\right]$, where ($a$ - b) is the range. Thus, total estimated variance for n weighed fish is n*Var or n*0.0833. To derive total estimates and total variances of these biomass estimates I sum the estimates and variances of the captured and non-captured fish using the FPCM estimator. To create a confidence interval, the total estimated variance, including the estimated variance of non-captured fish $(\widehat{W}_{non-captured})$ and variance of all weighed fish $\left(W_{weighed}\right)$, is incorporated into the lognormal 95% CI estimator provided above.

Estimates for Fish Captured but Not Weighed

Often biologists weigh only a portion of captured fish and develop length-weight regression relationships to predict weights for fish that are not weighed. To account for this situation I add a component to estimate biomass for fish that are captured and measured (total length; TL) but not weighed, according to the formula $\widehat{W}_{\text{tot}} = W_{\text{weighed}} + \widehat{W}_{\text{non-weighed}} + \widehat{W}_{\text{non-captured}}$, where $\widehat{W}_{\text{tot}}$ is the total estimated weight, W_{weighed} is the weight of all weighed fish, $\widehat{W}_{\text{non-weighed}}$ is the predicted weight of all captured fish with length measurements but no weights, and $\widehat{W}_{\text{non-captured}}$ is the estimated weight of fish not captured. I refer to this method as the FPCM_{reg} method to indicate it uses the FPCM estimator for non-captured fish.

Length-weight regression models are used to predict the weight of each fish whose length was measured but that was not weighed ($\widehat{W}_{\text{non-weighed}}$). For comparison with existing literature, I used $\log_{10}$ transformations of both lengths and weights (Anderson and Gutreuter 1983) in length-weight regressions. Length-weight regression models are developed for each species, by stream and sample date, using all captured fish for which length and weight data were available.

Variances associated with estimated weights predicted using length-weight regressions are estimated using the formula to estimate the variation of log weight:

$\hat{V}\left(log_{10}\widehat{W}\right) = \widehat{MSE} + \hat{V}\left(\hat{\beta}_0\right) + \left[2 * (log_{10}L) * Cov\left(\hat{\beta}_0 * \hat{\beta}_1\right)\right] + \left[(log_{10}L)^2 * V(\hat{\beta}_1)\right]$, where $log_{10}\widehat{W}$ is the $\log_{10}$ transformation of weight, $\widehat{MSE}$ is the mean squared error of the regression, $\hat{V}(\hat{\beta}_0)$ is the variance of the regression intercept, $log_{10}L$ is the log-10 transformation of measured fish length, $Cov(\hat{\beta}_0 * \hat{\beta}_1)$ is the regression covariance of slope and intercept, and $\hat{V}(\hat{\beta}_1)$ is the variance of the regression slope (Neter et al. 1996). Variance estimates computed in the log-scale are then back-transformed to estimate the variance for the predicted weights of the non-weighed fish using the formula: $\hat{V}(\widehat{W}) = (10^{(v*c)} - 1) * (10^{(2*x)+(v*c)})$, where *v* is the log-variance estimate of the predicted weight, *c* is a constant that is $\log_n(10)$, and *x* is the predicted $\log_{10}(W_{\text{non-weighed}})$ estimate. I assume that the sample of weighed fish used to develop the length-weight regression covers the full range of fish sizes and weight variation in the population.

Simulations

A dataset of 1,172 fish lengths and weights of brook trout (TL > 75 mm; range 76 to 245 mm) collected over five years in one stream represents the potential fish population (Appendix A). I assume that this dataset represents a typical distribution of lengths and weights for trout in headwater tributaries. I conduct 5,000 simulations (1,000 each for 5 different random draws of the true population) for each combination of eight different true population sizes (10 to 1,000), eight different capture probabilities (0.3 to 0.95), and four potential number of removal efforts (2 to 5 removals; Figure 2.1). I estimate population number (using removal estimators) and biomass using the two different estimators (OLD and FPC). A binomial distribution of each of the eight designated "true" capture probabilities (0.3 to 0.95) is used to select the fish captured from the true population for each removal pass. Fish are drawn from the true population without replacement to simulate removal of fish during each removal pass for two to five removal efforts. I assume a constant capture probability among fish and removals. I later discuss potential violations of this assumption. These simulations resulted in a total of 1,280,000 simulations (product of eight population sizes, eight capture probabilities, four removal efforts, and 5,000 replications).

The program "R" is used to run these simulations (R Development Core Team 2009). Maximum likelihood population estimates are made using the "deplet" function within the "fishmethods" package for "R" that assumes a constant capture probability (Nelson 2009). Variances of removal population estimates are computed using the estimator of Otis et al. (1978:108) originally recommended by Zippin (1958). For each simulation, estimates and variances of population number and biomass are computed using the three different estimators. I did not apply the FPC_{reg} estimator in these simulations.

Field Estimates

Removal population estimates were made in headwater stream sections using a maximum likelihood estimator (Van Deventer and Platts 1989). This estimator assumes a constant capture probability and is similar to the estimator used in simulations above. Fish were captured using Smith-Root® BP-15, BP-12, and SR-24 backpack electrofishers operated at voltages in the range of 100 to 600 V, frequencies under 50 Hz, and pulse widths less than 2 μsec to maximize the number of fish captured while minimizing injury to fish caused by the shock (Dwyer et al. 2001). An electrofishing crew consisted of either two or three people. One crewmember wore the backpack shocker and shocked using a wand anode while dragging a cable cathode. A second crewmember was the primary dip netter who followed the shocker and netted all stunned fish. When available, a third crewmember held a dip net in the stream channel below the two other crewmembers and carried a mesh bucket for transporting captured fish.

Either block nets or fencing material (6.5 mm mesh) were installed, or physical breaks were present, at sample section boundaries to prevent or limit movement of fish into and out of the sample sections. Two to five electrofishing removals were made in each sample section. The assumption of population closure is met by 1) using either block fences or nets at the upper and lower ends of sample sections, or locating sections so they had shallow riffles or velocity barriers at their upper and lower boundaries, 2) using a second netter during most sampling to prevent fish from moving downstream, 3) sampling relatively long sample sections relative to the stream size (section lengths were usually at least 30 times the average wetted width and almost all sample sections were longer than 50 m), and 4) the relatively short time it takes to complete all removal passes (White et al. 1982). I acknowledge that for those sections without block fences, some potential fish movement could have occurred into or out of the sample section during sampling (e.g., Peterson et al. 2005; however, for an alternative view see Young and Schmetterling 2004). If fish moved into or out of sample sections during sampling, removal population estimates could be biased.

I conducted 715 individual estimates in 99 individual streams throughout the Northern Rocky Mountains in Montana. I only include estimates where at least ten fish 75 mm TL and longer were captured. All captured fish were weighed in 619 estimates and some captured fish were not weighed in 96 estimates. Estimates are made for six salmonid species, including brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, bull trout *Salvelinus confluentus*, and mountain whitefish *Prosopium williamsoni*, but the species which were most commonly estimated are cutthroat trout (westslope *O. clarkii lewisi* and Yellowstone *O. c. bouveri* subspecies) and brook trout *Salvelinus fontinalis*. All estimates are for fish 75 mm TL and longer, and few fish exceeded 300 mm. Mean lengths and widths of sample sections were 142 m and 2.8 m.

Removal estimators under-estimate true abundances, especially when only two removals are made and capture probabilities are less than 0.8 (White et al. 1982; Riley and Fausch 1992). Three removals reduce estimate bias, but do not eliminate it (Riley and Fausch 1992; Peterson et al. 2004). Of the 619 removal population estimates I conducted where all captured fish were weighed, 394 (63%) were two-removal, 200 (32%) were three-removal, and 25 (4%) were four-removal estimates. Of the 394 two-removal estimates, estimated capture probabilities were at least 0.7 for 346 estimates (88%) and at least 0.8 for 274 estimates (70%). For these 619 removal population estimates relatively high proportions (mean = 0.96; SD = 0.07) of the estimated populations were actually captured and weighed, reflecting the relatively high capture probabilities I estimated for each species (mean = 0.75; median = 0.78). For field estimates of biomass I assume that capture probabilities were constant and removal estimators provide unbiased estimates of population numbers. I explore relaxation of the latter assumption using simulated data.

The FPCL, FPCM, and OLD methods were used to estimate biomass and its variance for the 619 estimates where all captured fish were weighed. For the 96 estimates where a portion of the captured fish was not weighed, the FPCL, $FPCM_{reg}$ and OLD methods were used to estimate biomass. For the FPCL and OLD methods the average weight of fish from the specific sample section was used when possible; however, for over half of the estimates (56 or 58%) I used the mean weights of fish from adjacent reaches that were weighed during the same week. For the $FPCM_{reg}$ biomass estimates, weights for those captured fish that were not weighed were estimated using $\log_{10}$(length) to $\log_{10}$(weight) prediction regressions developed for the same species within the same creek where estimates were made. In most of these cases a sub-sample of captured fish was weighed and length-weight regressions were developed from this subsample. Sub-samples of weighed fish were always taken during the same sample week within 2 km of the sample section where fish weights were estimated by prediction. However, in a few cases length-weight regressions for the sampled stream were developed from fish captured over several years, but within the same late summer time period.

<u>Data Analyses</u>

Population and biomass estimates for both simulated and field data were not normally distributed because of both a positive skew and a few extremely high values. I provide box plots of population estimates for some of the simulated data to illustrate these distributions. Because these data were not normally distributed, I use median values to compare performances of the three estimators.

Performance of the three biomass estimators is evaluated using coefficients of variation (CVs), square-roots of the mean square error (root-MSE), and coverages of the true biomass by 95% CIs. CVs are computed as the square-root of the variance divided by the estimate and are compared among methods for both field and simulated data. Mean squared error (MSE) accounts for both bias and variance (MSE = bias^2 + variance). Lower and upper 95% CI bounds around the estimated biomass were computed for each simulation data trial. The proportion of trials for which the 95% CIs covered the true biomass is reported by capture probability, population size, and number of removal efforts.

Because CV data were not normally distributed, nonparametric Wilcoxon sign-ranked tests are used to test for significant differences between OLD, FPCL, and FPCM CVs. Frequency distributions of CVs for biomass estimates are compared among the OLD, FPCL, and FPCM methods for the simulated data and field data for which all captured fish were weighed, and among the OLD, FPCL, and $FPCM_{reg}$ methods for the field data where a portion of the captured fish were not weighed. For simulation data, median biases in population and biomass estimates are standardized by subtracting the true population or biomass from the estimates and dividing by the true population or biomass. A similar procedure is followed to standardize the root-MSEs for simulated data. Median CVs for simulated data were also computed within each capture probability, population size, and removal effort combination for the OLD, FPCL, and FPCM methods and compared. Coverages of the 95% CIs for biomass estimates using the three methods (OLD, FPCL, and FPCM) were compared.

Results

Simulations

All the fish were captured on the first pass in 13,686 simulation trials for two-removal estimators (4%), 11,024 trials for three-removal estimators (3%), 248 trials for four-removal estimators (<1%), and 10,482 trials for five-removal estimators (3%) where all the fish were captured on the first pass. When all fish were captured on the first pass for two-removal trials the first removal catch was assumed to be the population estimate and its variance was assumed to be zero. Two-removal population estimates could not be made for many simulations (n=15,214; 5%) and a few three-removal simulations (n=6; <1%) because of non-declining catches, especially when both true populations and capture probabilities were low. The numbers of valid population estimates for two-removal efforts, by true capture probability-true population combination, are reported to show how often invalid estimates occurred out of the 5,000 potential simulations (Figures 2.2 through 2.5). Computation of valid population estimates was possible for all four- and five-removal estimates. If one or no fish was captured it was not possible to compute the variance associated with mean weights and estimate the variance of biomass estimates. This occurred infrequently for two-removal estimates (n=56) and only once for three-removal estimates, and these trials are excluded. More than one fish was always captured in four- and five-removal simulations.

Bias existed in estimates of population abundances and varied depending upon the number of removals, true capture probability, and true abundance (Figures 2.2 through 2.7). Abundance estimates were biased low when capture probabilities were low, few removals were made, and the true abundance was low. Conversely, abundance estimates were biased high for two-removal estimates when capture probabilities were 0.7 to 0.9 and true abundances were low (≤ 25; Figure 2.6). The distributions of biases were skewed with some estimates being much higher than the true abundances, especially if capture probabilities were low and true abundances were high. This skew was illustrated by how the mean and median values differed from the true abundances and by the number of outliers (Figures 2.2 and 2.3 and Appendix B). Estimated abundances were much higher than true abundances when less than 50% of the estimated population was captured (Figures 2.8 and 2.10). When the ratio of captured fish to the number estimated was at least 70%, deviations of estimated abundances from true abundances were centered close to zero and most deviations approached zero as this ratio went up.

I tried bias-correcting the population estimates using both the median and mean difference between the known true population and the estimated population for each combination of capture probabilities and true populations by adding these differences to the estimated population for each simulation within that capture probability-true population group. This bias-correction method requires knowing the true population. I considered median differences to be better than mean differences because median values better reduced the effect of the highly skewed extreme values on the estimates of bias. Median biases for both mean and median bias-corrected estimates were slightly lower than uncorrected estimates, but the median bias-corrections generally resulted in slightly lower biases than mean bias-corrections (Table 2.1).

I also attempted to predict bias in the population estimates using estimates of the probability of capture and population size within a multiple regression model. I wanted a method that would allow for predicting bias when the true capture probability and true population were unknown. Unfortunately, my exploration of this method indicated that the prediction ability was poor (R^2 values were less than 0.5) for efforts involving three or more removals, and although the prediction ability for two-removal efforts was reasonable ($R^2 = 0.78$), the variance associated with predicted bias-corrected estimates for two removals was high (regression $MSE = 55.6$).

Biases in estimated biomass using either uncorrected or bias-corrected population estimates were similar to the biases in the uncorrected or bias-corrected population estimates (Table 2.1). Because all attempts to bias-correct population estimates resulted in only slight improvement in bias-reduction in biomass estimates and bias was only a major problem when capture probabilities were low (Table 2.1), I report uncorrected population number estimates for the remainder of these analyses.

Estimates of biomass were the same for the OLD, FPCL, and FPCM methods. However, estimated variances were quite different among the three methods. The FPCL and FPCM methods had CVs of biomass that were nearly identical and their CVs were significantly narrower than the OLD method (Wilcoxon sign-ranked test; Figures 2.11

and 2.12). Because FPCL and FPCM results were nearly identical, I compare FPCL results to the OLD method and ignore the FPCM results unless they are different from FPCL results. Median CVs generally decreased as capture probabilities, population size, and number of removals increased (Figures 2.13 and 2.14). For the FPCL method with two-removal efforts, CVs were less than 50% of the biomass estimates for all population sizes for capture probabilities of 0.4 and declined further as capture probabilities increased (Figure 2.13). For three-removal efforts, CVs for the FPCL method fell below 5% of the biomass estimate if capture probabilities were 0.7 or higher. In contrast, estimated biomass CVs for the OLD method were usually higher than 80% for true population sizes above 18 (Figures 2.13 and 2.14).

Proportional root-MSEs were much lower for the FPCL method than the OLD method (Figures 2.15 and 2.16; Appendix C). This improvement was primarily caused by the reduction in estimated variance provided by the FPCL method (see Figures 2.13 and 2.14). Proportional root-MSEs for the FPCL method were less than 20% of biomass estimates at capture probabilities of 0.7 and higher for two-removal estimates and less than 12% of biomass estimates at capture probabilities higher than 0.6 for three-removal estimates.

True biomasses fell within FPCL 95% CIs in about 85 to 96% of the trials when capture probabilities were at least 0.5 and true populations were over 25, whereas coverage for the OLD method was nearly 100% (Figures 2.17 through 2.20). Coverages of the FPCL 95% CIs declined as capture probabilities increased over 0.8 for lower population sizes, but coverages of the FPCM 95% CIs did not. Estimates of 95% CIs for the FPCM method covered true biomasses close to the nominal 95% level across a relatively wide range of true population sizes and capture probabilities over 0.5. Estimated 95% CIs for the OLD method were much wider than those for the FPCL and FPCM methods, often ranging from near zero to twice the actual biomass. Coverages of the true biomass by the 95% CIs of both FPC methods generally increased as the number of removals increased (Figures 2.17 through 2.20).

Field Estimates

Distributions of the CVs for estimates of biomass from the field data illustrated that variances computed using the FPCL and FPCM methods were much lower than those computed using the OLD method (Figure 2.21). For the 619 biomass estimates where all captured fish were weighed, the median CV for the FPCL method (0.048) was significantly lower (Wilcoxon sign-ranked test; $P < 0.001$) than that of the OLD method (0.758; Figure 2.21, top). Median CV estimates for the FPCL (0.048) and FPCM (0.049) methods were not significantly different when all fish were weighed (Wilcoxon sign-ranked test; $P = 0.377$) and the distributions of the CVs for these two methods were similar (Figure 2.21, top). When various portions of captured fish were estimated using length-weight regression relationships, the $FPCM_{reg}$ method had significantly lower CVs (median = 0.043; Wilcoxon sign-ranked test; $P < 0.001$, n=96) than the OLD method (median = 0.817; Figure 2.21, bottom). Because the FPCL method relied on a similar variance estimator to that of the OLD method when many fish were not weighed, this method performed similarly to the OLD method when relatively low proportions of captured fish were weighed (both medians = 0.817; Wilcoxon sign-ranked test; P = 0.229).

Discussion

Both the FPCL and FPCM methods provide a significant improvement for estimating the precision of biomass estimates when all captured fish are weighed as performance of these two methods was nearly identical (Figures 2.11 through 2.15). Discrepancies between the FPCL and FPCM methods could be attributed to the fact that the FPCM method included measurement error, whereas the FPML method did not. The 95% CIs of the OLD method were much too wide with most covering 100% of the true biomass. Such wide CIs make it difficult to determine if statistically significant changes have occurred (Dauwalter et al. 2009). The FPCM method appeared to be superior to the FPCL method, which had poorer coverage at capture probabilities over 0.8 (Figures 2.17 and 2.18). I suspect that poor coverage at the higher capture probabilities for the FPCL method was probably related to two factors. First, measurement error was omitted from this estimator. Secondly, estimates of variance were too low at high capture probabilities because the assumption of normality is probably violated.

I illustrated that the maximum likelihood removal estimator has inherent bias, and this bias is related to capture probability and population size. This bias is considerable when the number of fish captured is less than 50% of the population estimate; deviations of estimates were much lower when captured fish make up more than 70% of the estimate (Figures 2.8 through 2.10). Note that each of the graphs in Figures 2.9 and 2.10

represents about 320,000 data points most of which cluster close to the zero reference lines at catch/estimate ratios of 0.7 and higher. Bias of a population estimate caused by the estimator would probably not be extreme if the total number of organisms captured composed at least 70% of the estimate, assuming a constant capture probability.

Assumption of a constant capture probability among removal efforts and for all fish longer than 75 mm has been shown to be false under many field settings where capture probabilities may vary by removal pass, size of fish, or even among individual fish (Cross and Stott 1975; Otis et al. 1978; Mahon 1980; White et al.1982; Moore et al. 1983; Schnute 1983; Peterson and Cedarholm 1984; Riley and Fausch 1992; Peterson et al. 2004; Rosenberger and Dunham 2005). Better estimates of capture probabilities and population sizes could be obtained by predicting these estimates through modeling that uses habitat and fish metric covariates (Peterson et al. 2004; Rosenberger and Dunham 2005; Rivot et al. 2008). My finding that population estimation bias is related to capture probability and population size and that this bias becomes relatively small as estimated capture probabilities exceed 0.8 supports the conclusions of several other studies (White et al.1982; Riley and Fausch 1992; Sweka et al. 2006). Unbiased estimates can be obtained by releasing marked fish prior to conducting depletions (Carrier et al. 2009). Bias in removal population estimators accounted for almost all the bias in estimates of biomass (Table 2.1). Bias-correction of population abundance estimates is important because population estimates are used to estimate both biomass and variance in biomass. I assume that if one could estimate bias of removal population estimates accurately and precisely, and correct for it, a concomitant improvement in the estimates of biomass using either of the FPC methods would occur. Unfortunately, my attempts to bias-correct population estimates using regression modeling and through simulation proved unsatisfactory, both in terms of accuracy and precision. I also speculate, based on my exploratory attempts at regression-based bias-correction prediction, that variances associated with regression-prediction methods to bias-correct population estimates could be relatively high.

Precision of biomass estimates for the two FPC methods were much narrower than the OLD method. Precision of biomass estimates for the OLD method could probably be increased substantially if population and weight estimates were computed for narrow size groups, or age groups, and proportionally summed (Newman and Martin 1983). Unfortunately, it is usually impossible to make reliable population estimates for narrow length or age groups in small streams because of the relatively low population sizes in these streams. I suggest that the FPCM method is superior to the FPCL method because the FPCM method allows for the partitioning of variance and 95% CIs were more consistently closer to the nominal 95% level for capture probabilities above 0.6. The ability to partition variance with the FPCM method allows it to be used in conjunction with predicted weight estimates of fish that are measured, but not weighed, as I demonstrated with the $FPCM_{reg}$ method (Figure 2.21).

Gould and Pollock (1997) indicated that maximum likelihood estimators for estimating population numbers using removal methods were less biased and more precise than regression estimators. Estimating variances of population estimates using maximum likelihood estimates of the Zippin constant capture probability estimator (1958; cited in

Otis et al. 1978: 108) generally resulted in narrower variance estimates than variances estimated using the maximum likelihood estimator that did not assume constant capture probabilities (Otis et al. 1978: 113). I used the Zippin (1958) constant capture probability estimator to allow for consistent comparisons between two-removal estimates and estimates derived from more than two removals (Nelson 2009).

Length-weight models should, if possible, be developed for each individual population (i.e., stream or stream reach) and sampling period if they are used to estimate weights of fish that are captured but not weighed. A sampling period should be a relatively short time-period (i.e., one or two week period) to reduce seasonal differences in length-weight relationships caused by variability in weather and food availability. I recommend that at least 30 fish across the range of potential fish sizes in the population be used to develop models for each species; however, I do not have a statistically rigorous rationale for this suggestion. When several sections are sampled within a stream, and these sample sections constitute a single fish population, fish from all sections can be pooled to develop the length-weight regression for each species. In some cases length and weight information will not be available for 30 fish for a particular stream population. In these cases models can be developed from data, in decreasing preferential order, from the same stream during the same time period in a different year, from a regional sample during the same time period, or from a regional sample pooled over a single season.

Use of either of the FPC methods improves the precision of biomass estimates. The FPCM method is superior if some fish are measured but not weighed. This method will improve estimates of precision in any situation where a moderate to high proportion of the target organisms are captured during sampling, including mark-recapture estimates. I acknowledge that bias associated with removal population estimates is a concern and suggest that bias-correction be incorporated when conducting removal estimates (e.g., Peterson et al. 2004; Rosenberger and Dunham 2005) to provide better estimates of biomass and it variance. Where feasible, biologists should conduct three or more removal efforts in at least a portion of their sampling sites to determine if capture probabilities are constant or not. For the simulated data, where I assumed constant capture probabilities, I found that when capture probabilities were 0.7 or higher population numbers and biomass could be reasonably estimated, regardless of the level of effort.

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<u>Literature Cited</u>

Anderson, R. O., and S. J. Gutreuter. 1983. Length, weight, and associated structural indices. Pages 283-300 *in* L. A. Nielsen and D. L. Johnson, editors. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Bayley, P. B., and D. C. Dowling. 1993. The effect of habitat in biasing fish abundance and species richness estimates when using various sampling methods in streams. Polskie Archiwum Hydrobiologii 40:5-14.

Büttiker, B. 1992. Electrofishing results corrected by selectivity functions in stock size estimates of brown trout (*Salmo trutta* L) in brooks. Journal of Fish Biology 41:673-684.

Carrier, P., J. S. Rosenfeld, and R. M. Johnson. 2009. Dual-gear approach for calibrating electric fishing capture efficiency and abundance estimates. Fisheries Management and Ecology 16:139-146.

Chow, Y. S., H. Robbins, and H. Teicher. 1965. Moments of randomly stopped sums. Annals of Mathematical Statistics 36:789-799.

Cross, D. G., and B. Stott. 1975. The effect of electric fishing on the subsequent capture of fish. Journal of Fish Biology 7:349-357.

Dauwalter, D. C., F. J. Rahel, and K. G. Gerow. 2009. Temporal variation in trout populations: implications for monitoring and trend detection. Transactions of the American Fisheries Society 138:38-51.

DeLury, D. B. 1947. On the estimation of biological populations. Biometrics 3:145-167.

Dolan, C. R., and L. E. Miranda. 2003. Immobilization thresholds of electrofishing relative to fish size. Transactions of the American Fisheries Society 132:969-976.

Dwyer, W. P., B. B. Shepard, and R. G. White. 2001. Effect of backpack electroshock on westslope cutthroat trout injury and growth 110 and 250 days post-treatment. North American Journal of Fisheries Management 21:646-650.

Goodman, L. A. 1960. On the exact variance of products. Journal of the American Statistical Association 55:708-713.

Gould, W. R., and K. H. Pollock. 1997. Catch-effort maximum likelihood estimation of important population parameters. Canadian Journal of Fisheries and Aquatic Sciences 54:890-897.

Gutreuter, S., and D. J. Krzoska. 1994. Quantifying precision of in situ length and weight measurements of fish. North American Journal of Fisheries Management 14:318-322.

Hatch, R. W., P. M. Haack, and H. Brown, Jr. 1981. Estimation of alewife biomass in Lake Michigan, 1967–1978. Transactions of the American Fisheries Society 110:575–584.

Hayes, D. B., J. R. Bence, T. J. Kwak, and B. E. Thompson. 2007. Abundance, biomass, and production. Pages 327-374 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Jones, N. E., W. M. Tonn, G. J. Scrimgeour, and C. Katopodis. 2003. Productive capacity of an artificial stream in the Canadian Arctic: assessing the effectiveness of fish habitat compensation. Canadian Journal of Fisheries and Aquatic Sciences 60:849-863.

Krause, A. E., D. B. Hayes, J. R. Bence, C. P. Madenjian, and R. M. Stedman. 2002. Measurement error associated with surveys of fish abundance in Lake Michigan. Journal of Great Lakes Research 28:44-51.

Kruse, C. G., W. A. Hubert, and F. J. Rahel. 1998. Single-pass electrofishing predicts trout abundance in mountain streams with sparse habitat. North American Journal of Fisheries Management 18:940-946.

Leslie, P. H., and D. H. S. Davis. 1939. An attempt to determine the absolute number of rats on a given area. Journal of Animal Ecology 8:94-113.

Lewis, C. A., D. H. Schupp, W. W. Taylor, J. J. Collins, and R. W. Hatch. 1987. Predicting Great Lakes fish yields: tools and constraints. Canadian Journal of Fisheries and Aquatic Sciences 44:411–416.

Lohr, S. L. 1999. Sampling: design and analysis. Duxbury Press, Brooks/Cole Publishing Company, Pacific Grove, California.

Mahon, R. 1980. Accuracy of catch-effort methods for estimating fish density and biomass in streams. Environmental Biology of Fishes 5:343-360.

Mesa, M. G., and C. B. Schreck. 1989. Electrofishing mark-recapture and depletion methodologies evoke behavioral and physiological changes in cutthroat trout. Transactions of the American Fisheries Society 118:644-658.

Moore, S. E., B. Ridley, and G. L. Larson. 1983. Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. North American Journal of Fisheries Management 3:72-80.

Mullner, S. A., W. A. Hubert, and T. A. Wesche. 1998. Snorkeling as an alternative to depletion electrofishing for estimating abundance and length-class frequencies of trout in small streams. North American Journal of Fisheries Management 18:947-953.

Nelson, G. 2009. Fishmethods: fisheries methods and models in R. R package version 1.0-1. R Foundation for Statistical Computing, Vienna. Available: http://CRAN.R-project.org/package=fishmethods (August 2009).

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models, 4th edition. WCB McGraw-Hill, Boston.

Newman, R. M., and F. B. Martin. 1983. Estimation of fish production rates and associated variances. Canadian Journal of Fisheries and Aquatic Sciences 40:1729-1736.

Otis D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:1-135.

Peterson, J. T., R. F. Thurow, and J. W. Guzevich. 2004. An evaluation of multi-pass electrofishing for estimating the abundance of stream-dwelling salmonids. Transactions of the American Fisheries Society 133:462-475.

Peterson, J. T., N. P. Banish, and R. F. Thurow. 2005. Are block nets necessary?: movement of stream-dwelling salmonids in response to three common survey methods. North American Journal of Fisheries Management 25:732-743.

Peterson, N. P., and C. J. Cederholm. 1984. A comparison of the removal and mark-recapture methods of population estimation for juvenile coho salmon in a small stream. North American Journal of Fisheries Management 4:99-102.

Quinn, T. J.,II, and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available: http://www.R-project.org (May 2009).

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada, Ottawa.

Riley, S. C., and K. D. Fausch. 1992. Underestimation of trout population size by maximum-likelihood removal estimates in small streams. North American Journal of Fisheries Management 12:768-776.

Riley, S. C., R. L. Haedrich, and R. J. Gibson. 1993. Negative bias in removal estimates of Atlantic salmon parr relative to stream size. Journal of Freshwater Ecology 8:97-101.

Rivot, E., E. Prevost, A. Cuzol, J. L. Bagliniere, and E. Parent. 2008. Hierarchical Bayesian modelling with habitat and time covariates for estimating riverine fish population size by successive removal method. Canadian Journal of Fisheries and Aquatic Sciences 65:117-133.

Rodgers, J. D., M. F. Solazzi, S. L. Johnson, and M. A. Buckman. 1992. Comparison of three techniques to estimate juvenile coho salmon populations in small streams. North American Journal of Fisheries Management 12:79-86.

Rosenberger, A. E., and J. B. Dunham. 2005. Validation of abundance estimates from mark-recapture and removal techniques for rainbow trout captured by electrofishing in small streams. North American Journal of Fisheries Management 25:1395-1410.

Royall, R. M. 1970. On finite population sampling theory under certain linear regression models. Biometrika 57:377-387.

Scarnecchia, D. L., and E. P. Bergersen. 1987. Trout production and standing crop in Colorado's small streams, as related to environmental features. North American Journal of Fisheries Management 7:315-330.

Schnute, J. 1983. A new approach to estimating populations by the removal method. Canadian Journal of Fisheries and Aquatic Sciences 40:2153-2169.

Smith, S. J., and S. Gavaris. 1993. Improving the precision of abundance estimates of eastern Scotian Shelf Atlantic cod from bottom trawl surveys. North American Journal of Fisheries Management 13:35–47.

Sweka, J. A., C. M. Legault, K. F. Beland, J. Trial, and M. J. Millard. 2006. Evaluation of removal sampling for basinwide assessment of Atlantic salmon. North American Journal of Fisheries Management 26:995-1002.

Van Deventer, J. S., and W. S. Platts. 1989. Microcomputer software system for generating population statistics from electrofishing data - User's guide for Microfish 3.0. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, General Technical Report INT-254, Ogden, Utah.

White, G. C., D. R. Anderson, K. P. Burnham and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. U.S. Department of Energy, Los Alamos National Laboratory, Report LA-8787-NERP, Los Alamos, New Mexico.

Valiant, R., A. H. Dorfman, and R. M. Royall. 2000. Finite population sampling and inference: a prediction approach. John Wiley and Sons, New York.

Young, M. K., and D. A. Schmetterling. 2004. Electrofishing and salmonid movement: reciprocal effects in two small montane streams. Journal of Fish Biology 64:750-761.

Zippin, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22:82-90.

Table 2.1. Median proportional bias ([True - Estimated]/True) in population and biomass estimates for uncorrected and both median and mean bias-corrected population estimates by removal effort (*n*-removals) and capture probability (*p*).

Effort	Uncorrected		Median Bias-corrected		Mean Bias-corrected	
p	Population	Biomass	Population	Biomass	Population	Biomass
2-removals						
0.3	0.0867	0.0752	0.0660	0.0649	0.0660	0.0654
0.4	0.0233	0.0199	0.0133	0.0131	0.0140	0.0133
0.5	0.0000	-0.0038	0.0000	-0.0061	0.0000	-0.0060
0.6	0.0000	-0.0101	-0.0060	-0.0092	-0.0060	-0.0091
0.7	-0.0020	-0.0113	-0.0033	-0.0086	-0.0033	-0.0086
0.8	-0.0040	-0.0105	0.0000	-0.0025	0.0000	-0.0025
0.9	-0.0033	-0.0061	0.0000	0.0000	0.0000	0.0000
0.95	-0.0010	-0.0020	0.0000	0.0000	0.0000	0.0000
3-removals						
0.3	0.0540	0.0495	0.0320	0.0282	0.0380	0.0322
0.4	0.0200	0.0211	0.0000	0.0040	0.0040	0.0072
0.5	0.0080	0.0084	0.0000	-0.0023	0.0000	0.0000
0.6	0.0000	0.0011	0.0000	-0.0045	0.0000	-0.0024
0.7	0.0000	0.0000	0.0000	-0.0020	0.0000	-0.0005
0.8	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
0.9	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
0.95	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
4-removals						
0.3	0.0240	0.0233	0.0320	0.0282	0.0200	0.0171
0.4	0.0070	0.0077	0.0000	0.0040	0.0000	0.0017
0.5	0.0000	0.0003	0.0000	-0.0023	0.0000	0.0000
0.6	0.0000	0.0000	0.0000	-0.0045	0.0000	0.0000
0.7	0.0000	0.0000	0.0000	-0.0020	0.0000	0.0000
0.8	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
0.9	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
0.95	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
5-removals						
0.3	0.0120	0.0121	0.0080	0.0087	0.0100	0.0101
0.4	0.0000	0.0017	0.0000	0.0000	0.0000	0.0000
0.5	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
0.6	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
0.7	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
0.8	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
0.9	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
0.95	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

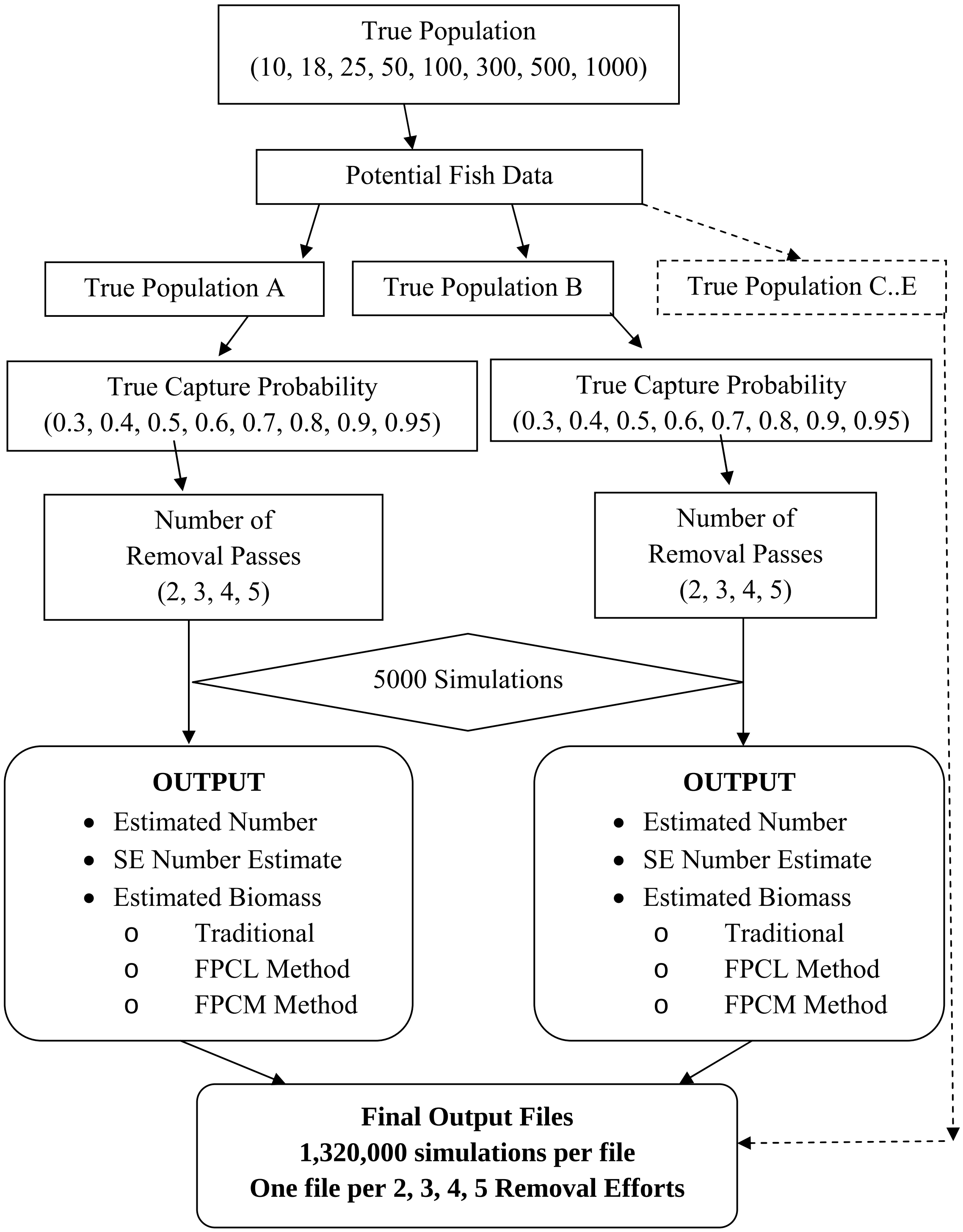


Figure 2.1. Simulation procedure used. Numbers in parentheses represent the true populations, capture probabilities, and number of removal passes for which simulations were done.

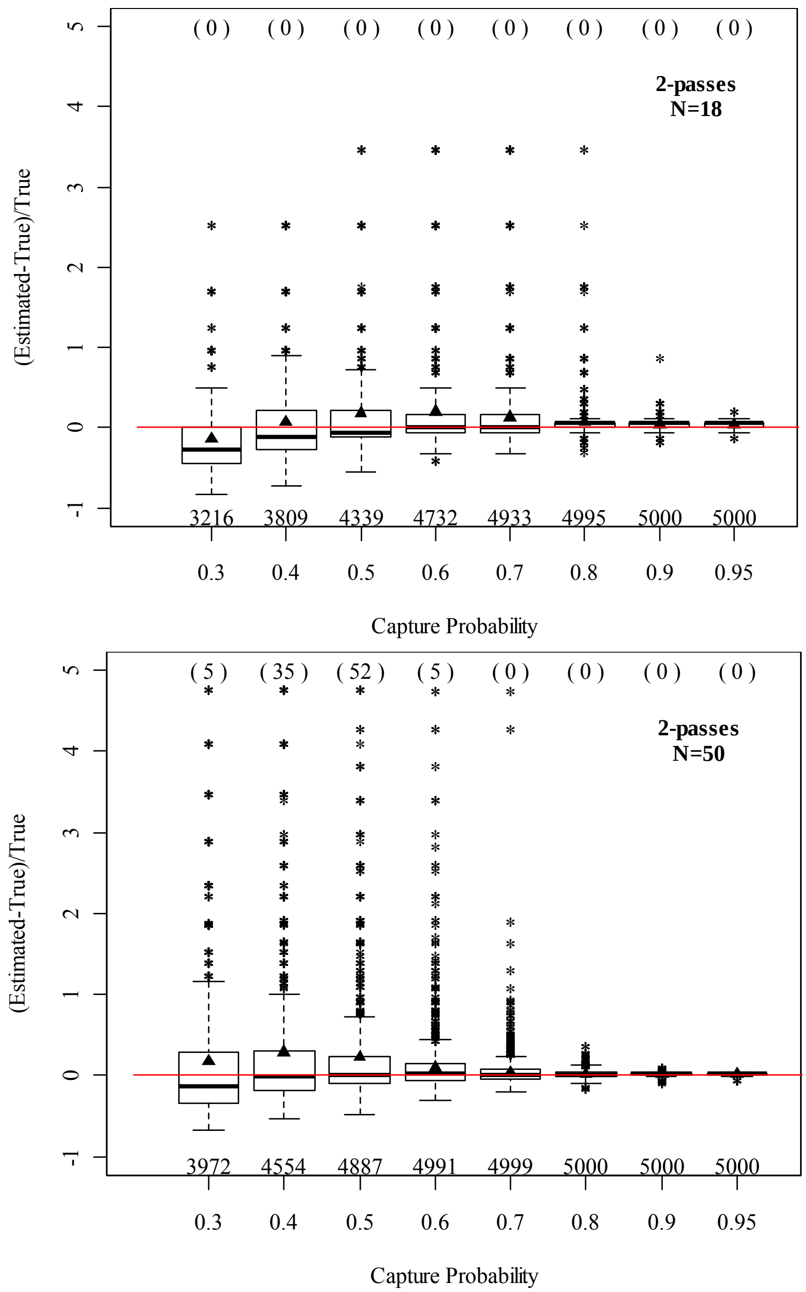


Figure 2.2. Proportional bias ([Estimate-True]/True) for 5,000 two-removal abundance estimate simulations by true capture probability (x-axis) and population abundances of 18 (top graph) and 50 (bottom graph) showing medians (bold lines), means (solid triangles), numbers of valid estimates (out of a possible 5,000, shown above each capture probability just above the x-axis), and number of upper outliers (above 5.0; near the top of graph in parentheses). Red line is reference for zero bias.

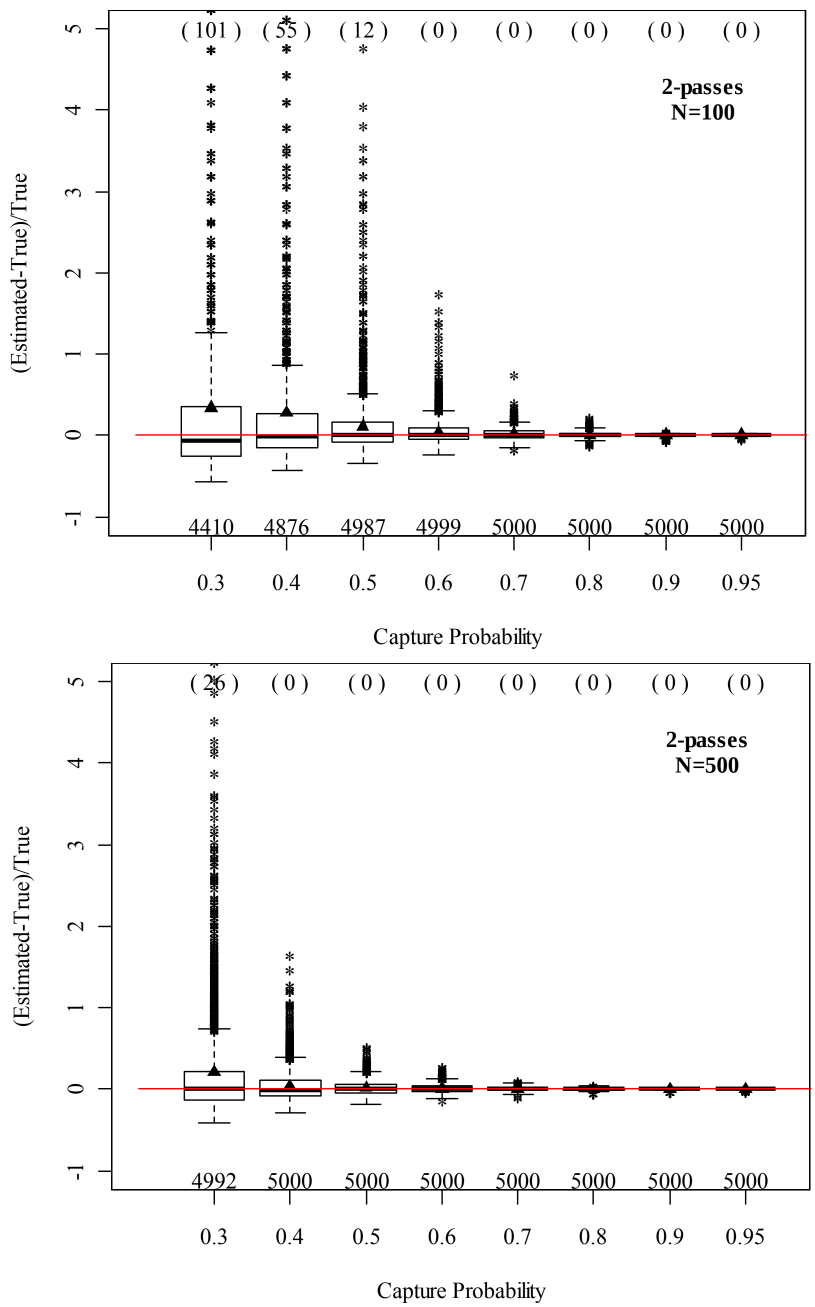
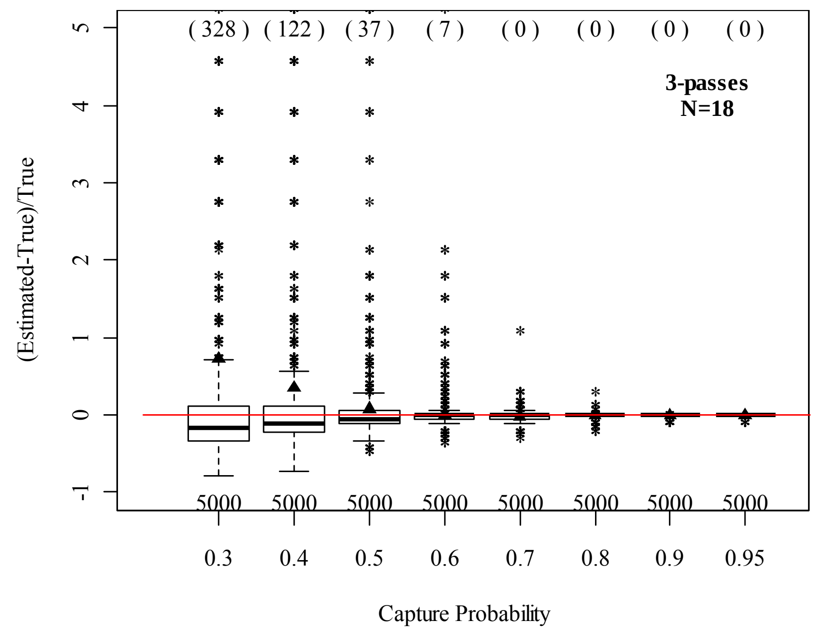


Figure 2.3. Proportional bias ([Estimate-True]/True) for 5,000 two-removal abundance estimate simulations by true capture probability (x-axis) and population abundances of 100 (top graph) and 500 (bottom graph) showing medians (bold lines), means (solid triangles), numbers of valid estimates (out of a possible 5,000, shown above each capture probability just above the x-axis), and number of upper outliers (above 5.0; near the top of graph in parentheses). Red line is reference for zero bias.



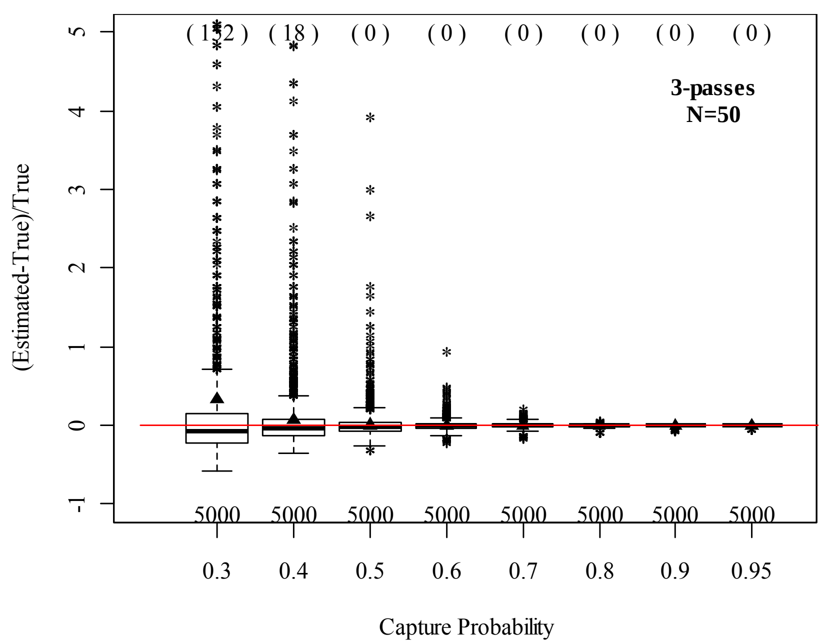
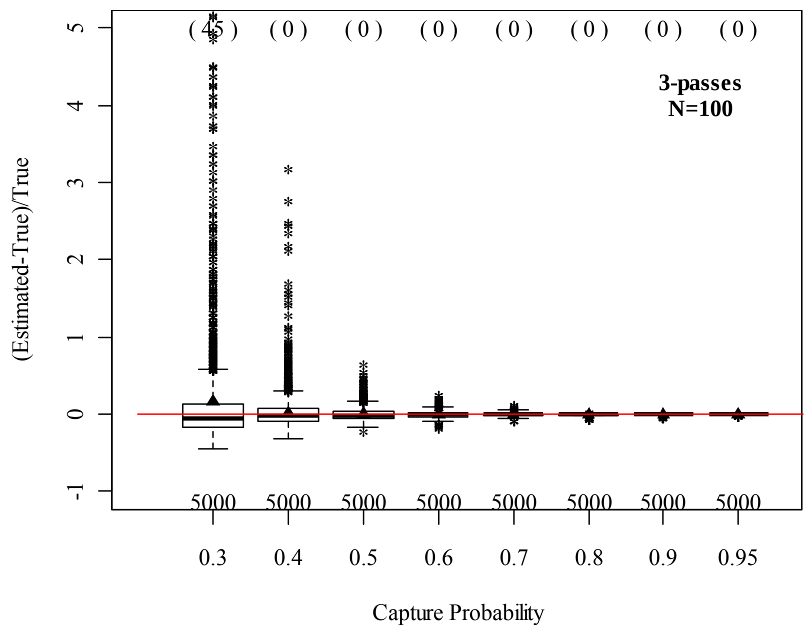


Figure 2.4. Proportional bias ([Estimate-True]/True) for 5,000 three-removal abundance estimate simulations by true capture probability (x-axis) and population abundances of 18 (top graph) and 50 (bottom graph) showing median (bold lines), mean (solid triangles), number of valid estimates (out of a possible 5,000 as shown as number above each capture probability just above the x-axis), and number of upper outliers (above 5.0; near the top of graph as numbers in parentheses). Red line is reference for zero bias.



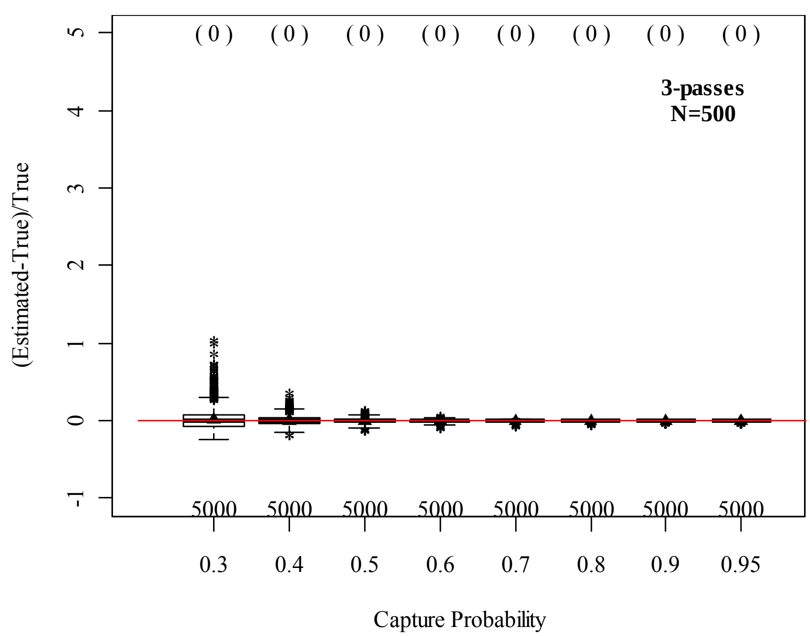


Figure 2.5. Proportional bias ([Estimate-True]/True) for 5,000 three-removal abundance estimate simulations by true capture probability (x-axis) and population abundances of 100 (top graph) and 500 (bottom graph) showing medians (bold lines), means (solid triangles), numbers of valid estimates (out of a possible 5,000, shown above each capture probability just above the x-axis), and number of upper outliers (above 5.0; near the top of graph in parentheses). Red line is reference for zero bias.

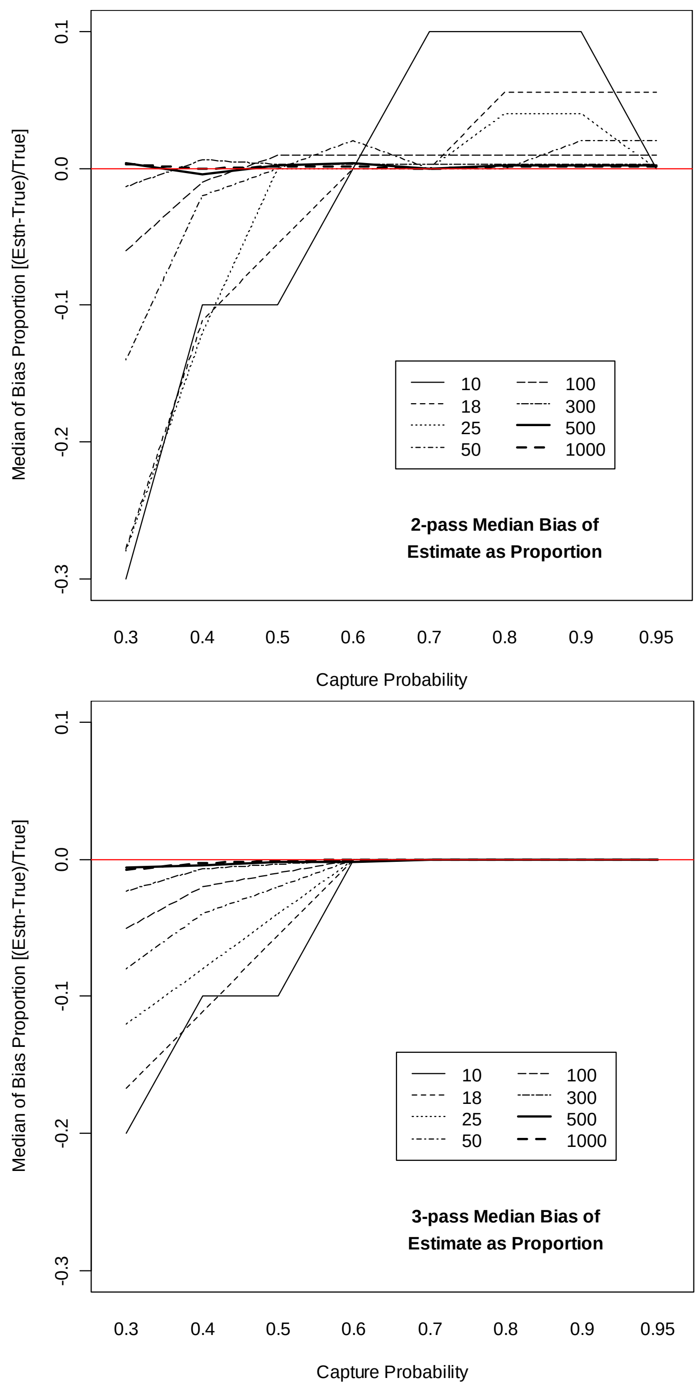


Figure 2.6. Median bias in estimated abundance as proportion of true abundance for two- (top graph) and three-removal (bottom graph) estimates for various levels of true capture probabilities (x-axis) and different true abundances (different lines on each graph) based on 5,000 simulations for each combination of true capture probability and true population abundance. Red line indicates zero bias.

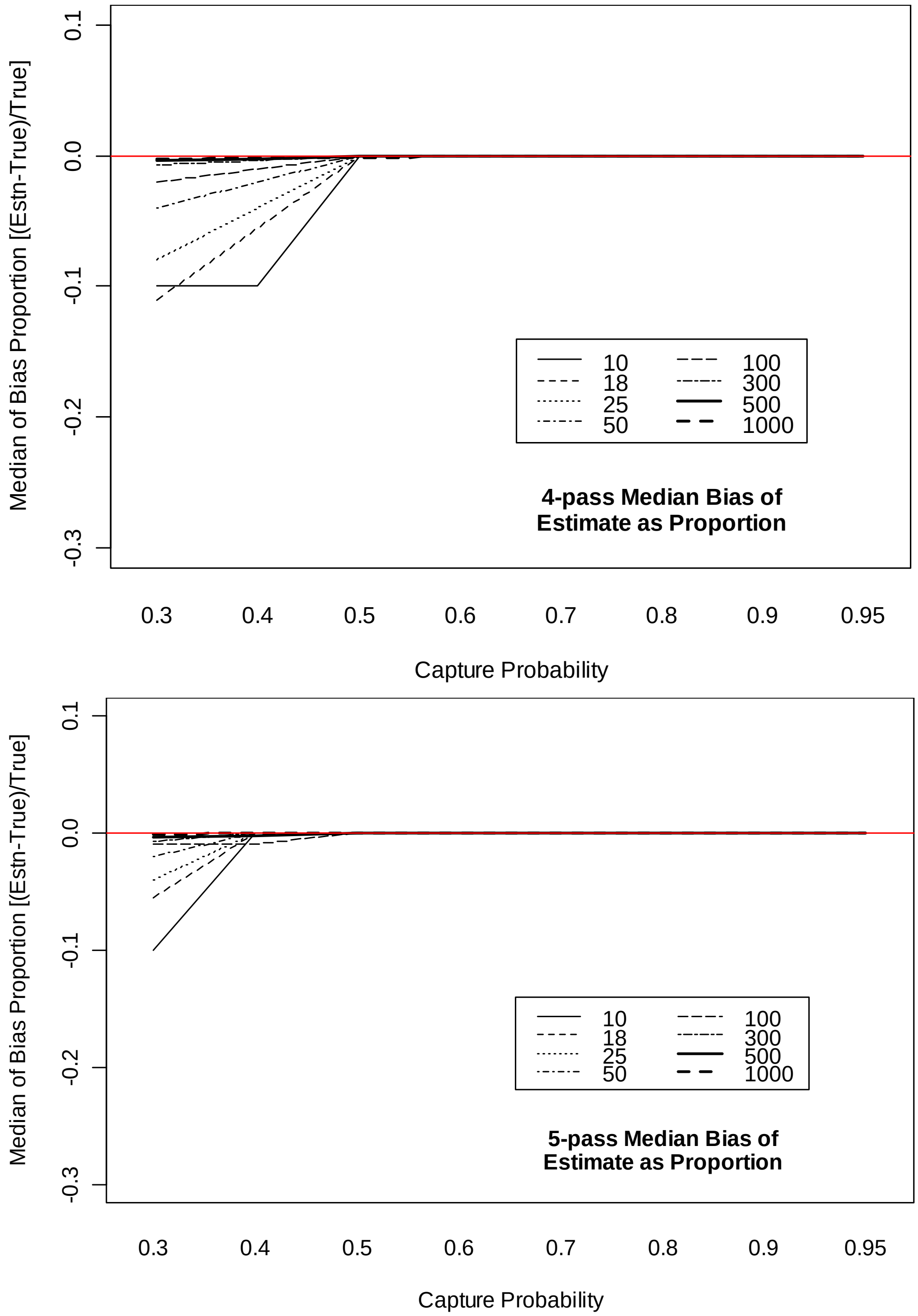


Figure 2.7. Median bias in estimated abundance as proportion of true abundancefor four- (top graph) and five-removal (bottom graph) estimates for various levels of true capture probabilities (x-axis) and different true abundances (different lines on each graph) based on 5,000 simulations for each combination of true capture probability and true abundance.

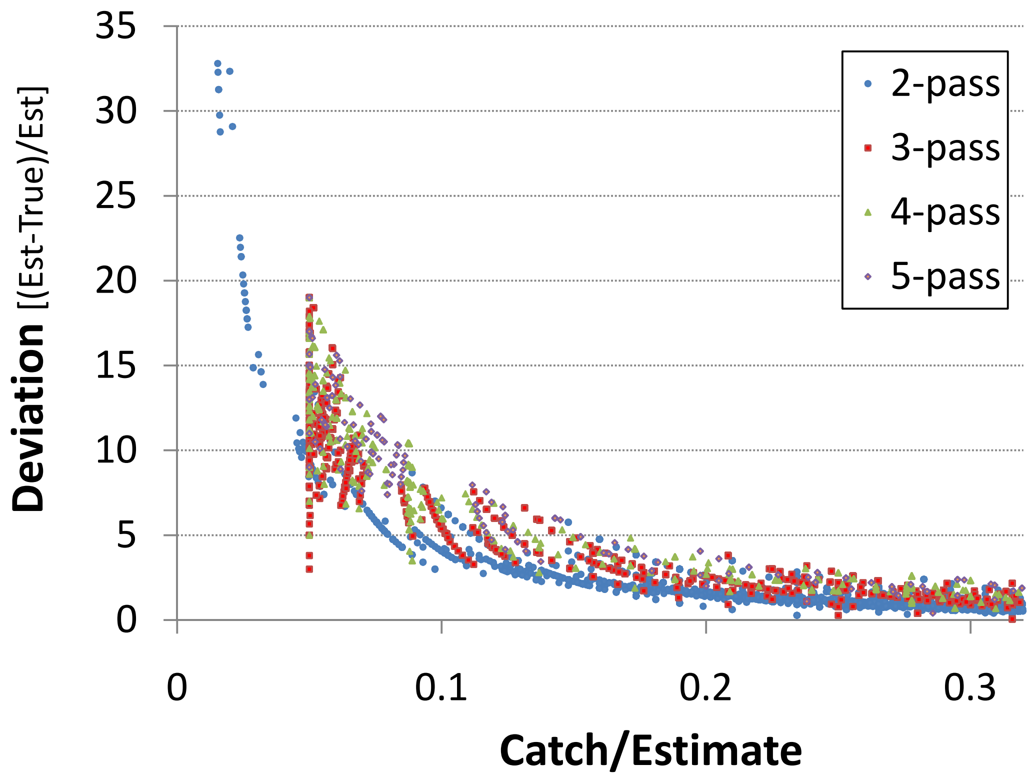


Figure 2.8. Relationship between deviations in abundance estimates from true abundances (y-axis) as a ratio of the number of fish captured to the abundance estimate (x-axis; Catch/Estimate) for two- through five-removal simulated data at catch/estimate ratios of 30% and less.

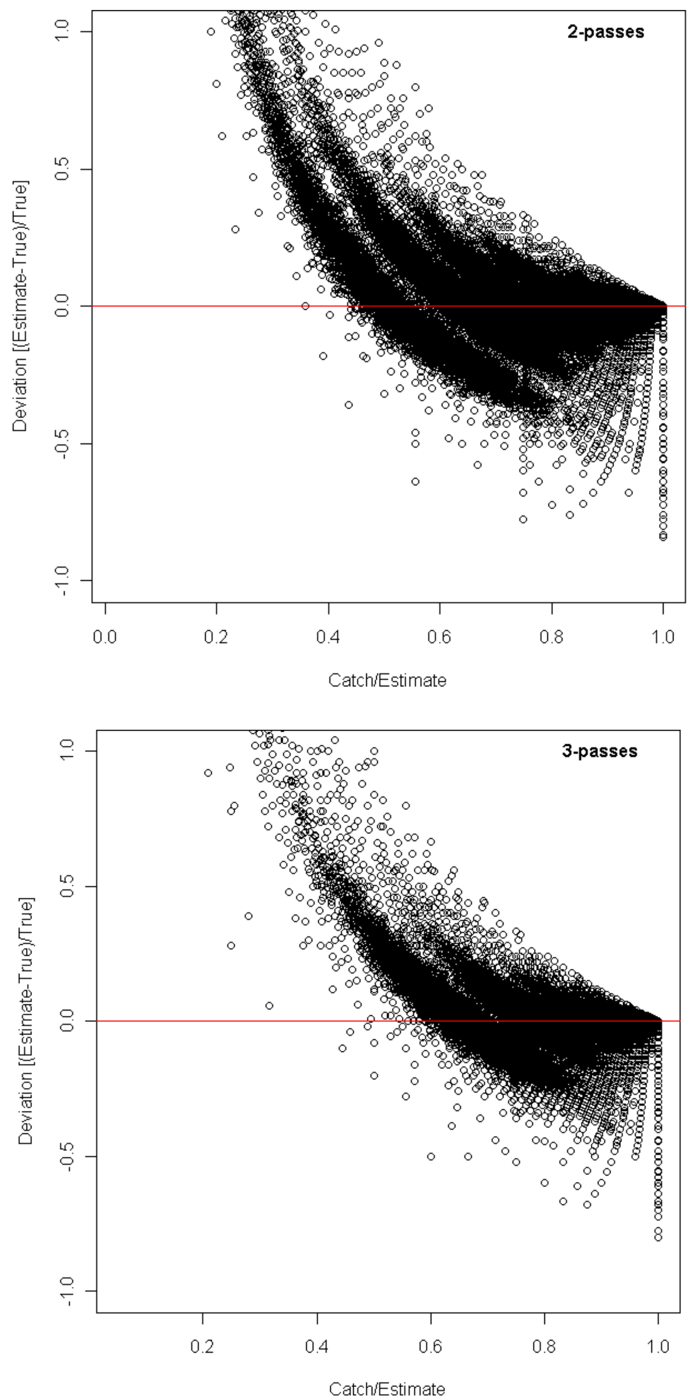


Figure 2.9. Relationship between deviations in abundance estimates from true abundances (y-axis) as a ratio of the number of fish captured to the abundance estimate (x-axis; Catch/Estimate) for simulated data for two- (top) and three-removal (bottom) passes. Red horizontal line at zero indicates no deviation.

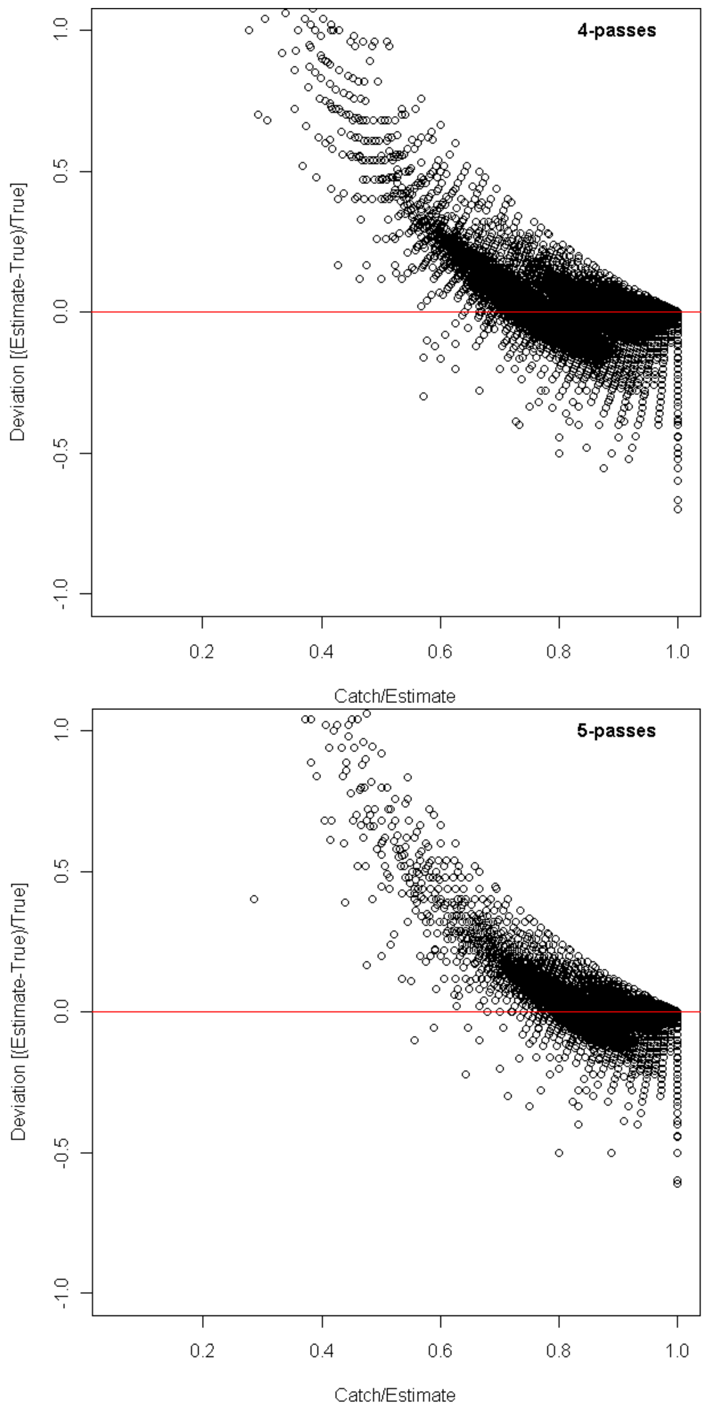
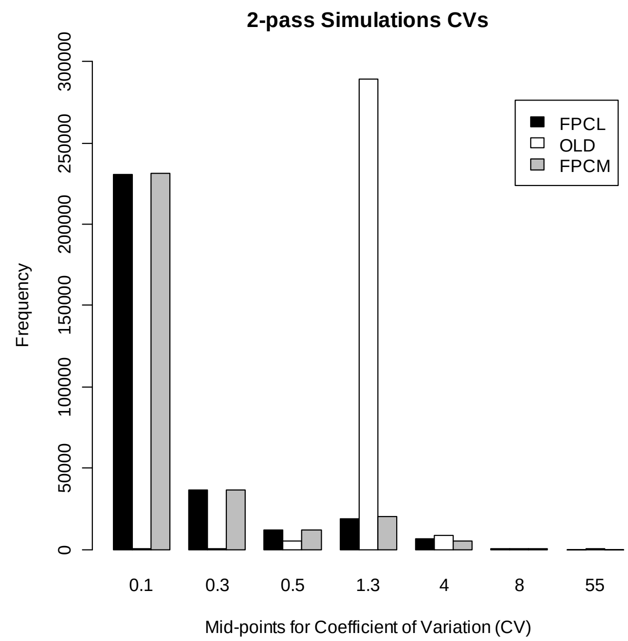


Figure 2.10. Relationship between deviations in abundance estimates from true abundances (y-axis) as a ratio of the number of fish captured to the abundance estimate (x-axis; Catch/Estimate) for simulated data for four- (top) and five-removal (bottom) passes. Red horizontal line at zero indicates no deviation.



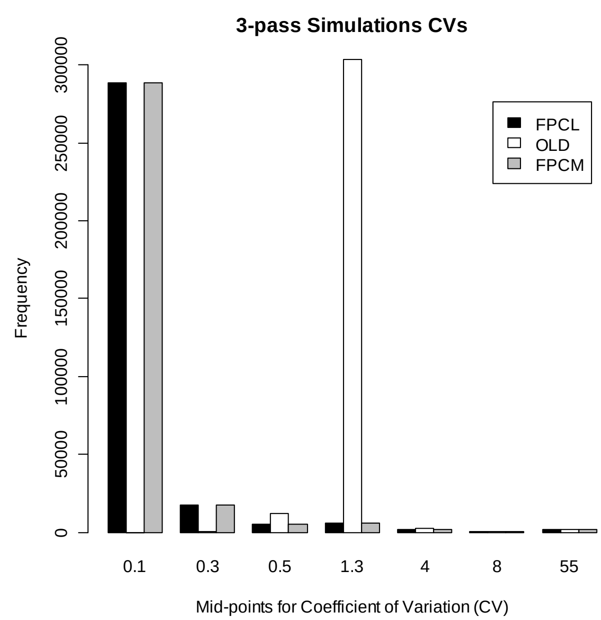


Figure 2.11. Distributions of the coefficients of variation (CV) for bias-corrected biomass estimates using the FPCL, FPCM, and OLD methods (see the text for definitions of these acronyms) for two- (top) and three-pass (bottom) removal estimates based on simulated data. Mid-points of CVs are shown on the x-axis.

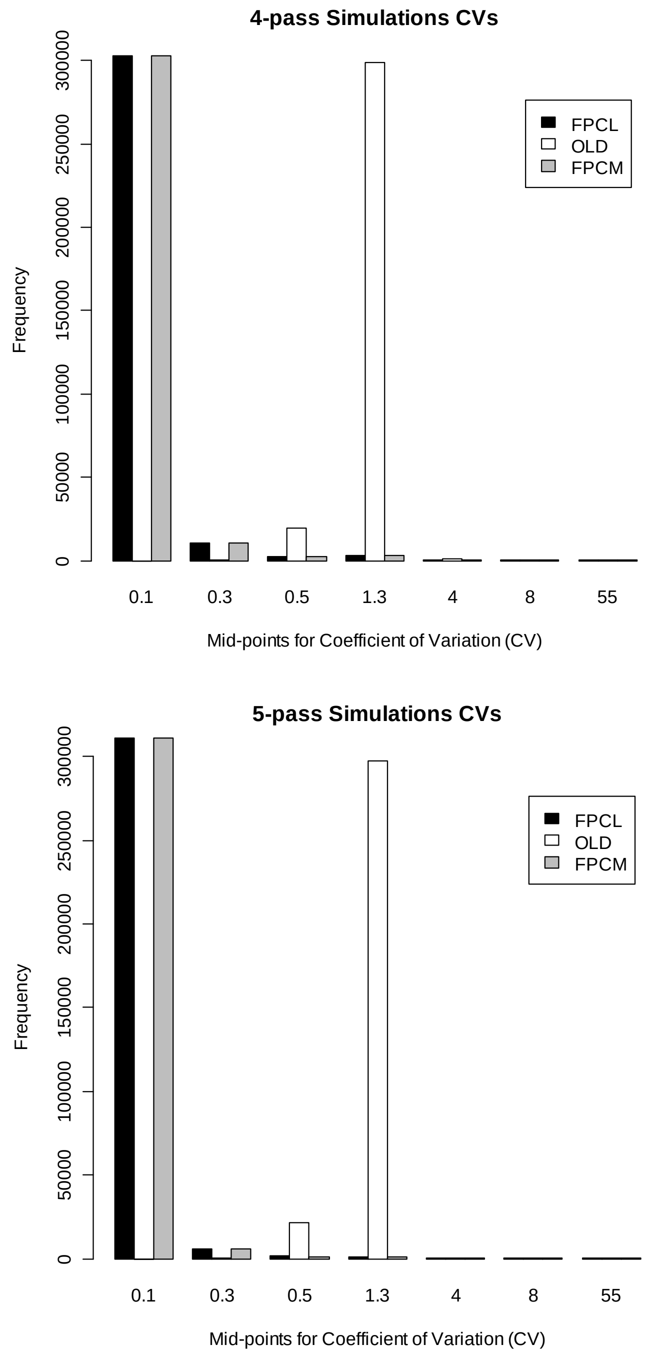


Figure 2.12. Distributions of the coefficients of variation (CV) for bias-corrected biomass estimates using the FPCL and OLD methods (see the text for definitions of these acronyms) for four- (top) and five-pass (bottom) removal estimates based on simulated data. Mid-points of CVs are shown on the x-axis.

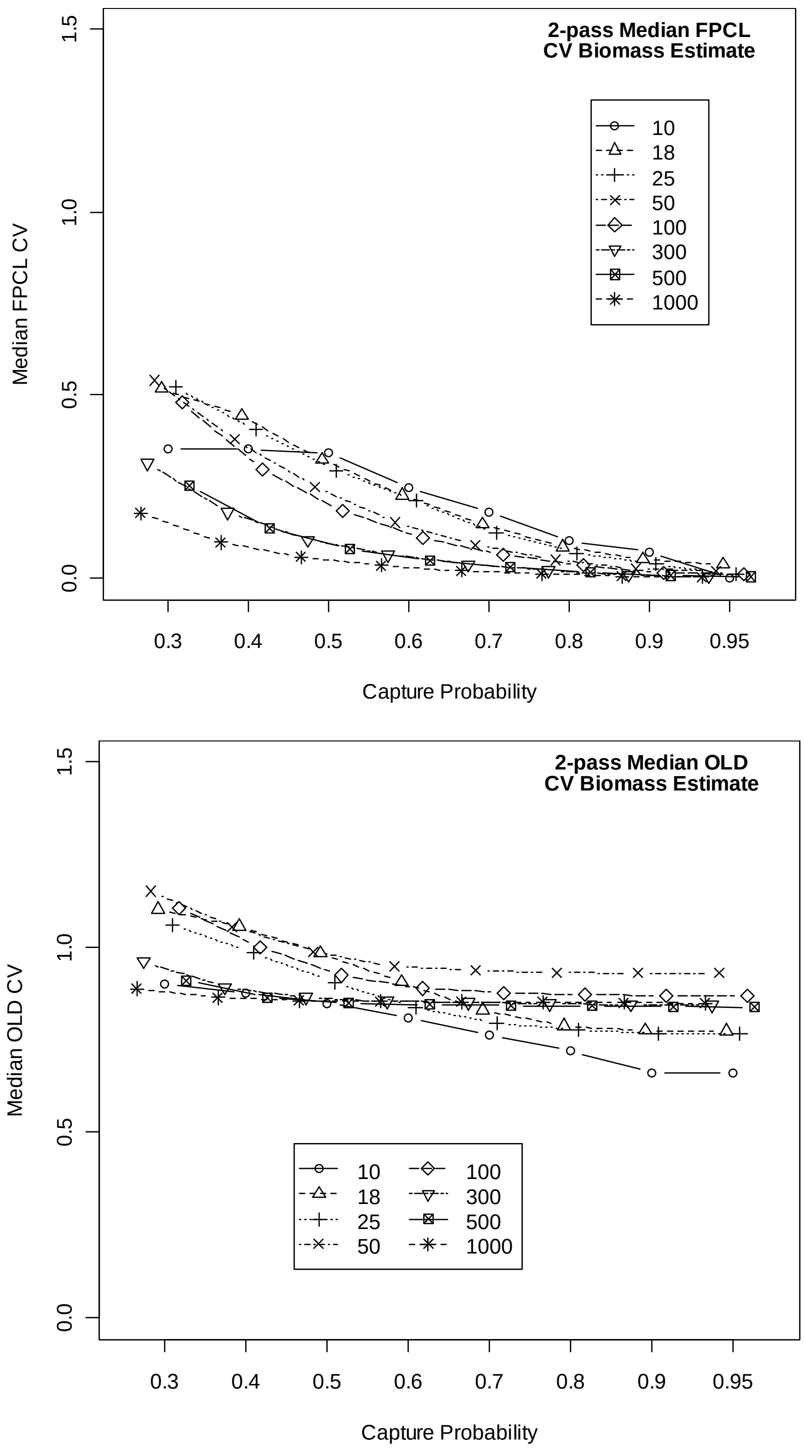
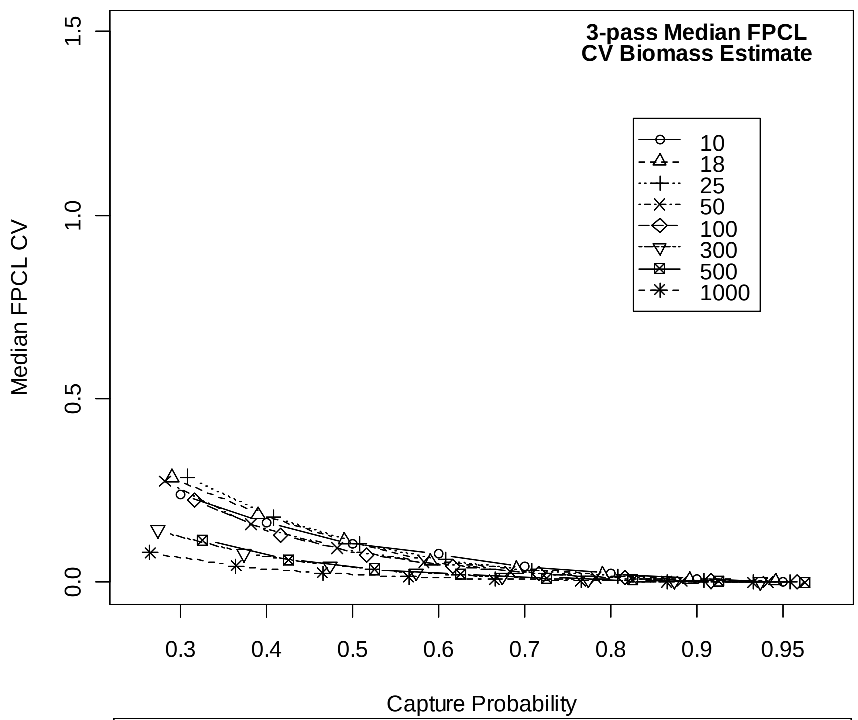


Figure 2.13. Median coefficients of variation (CV) by true capture probability (x-axis) and population size (different lines) of two-pass estimated biomass using bias-corrected population estimates for FPCL (top) and OLD (bottom) methods.



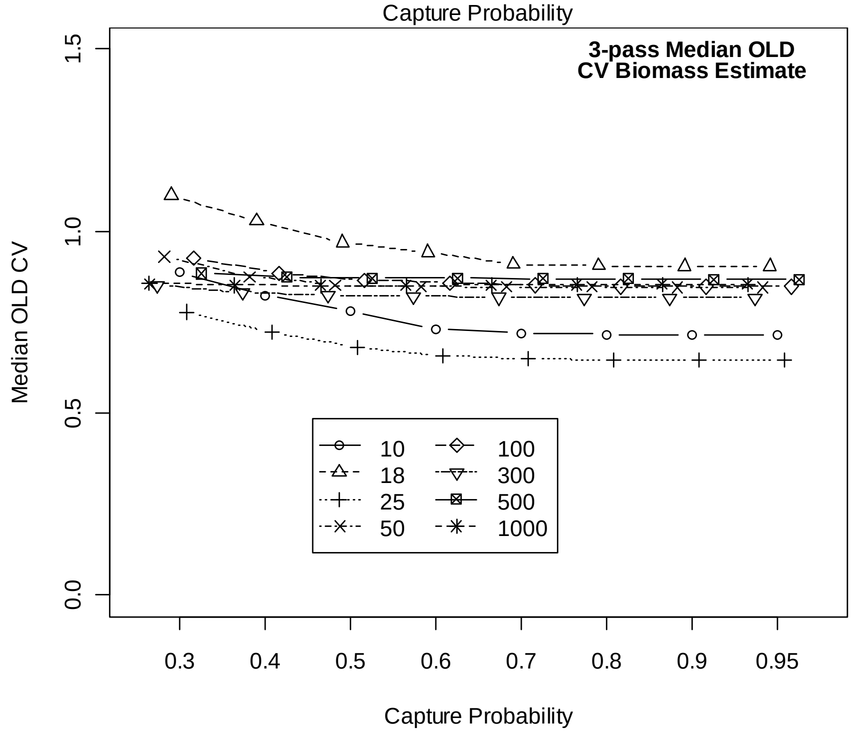


Figure 2.14. Median coefficients of variation (CV) by true capture probability (x-axis) and population size (different lines) of three-pass estimated biomass using bias-corrected population estimates for FPCL (top) and OLD (bottom) methods.

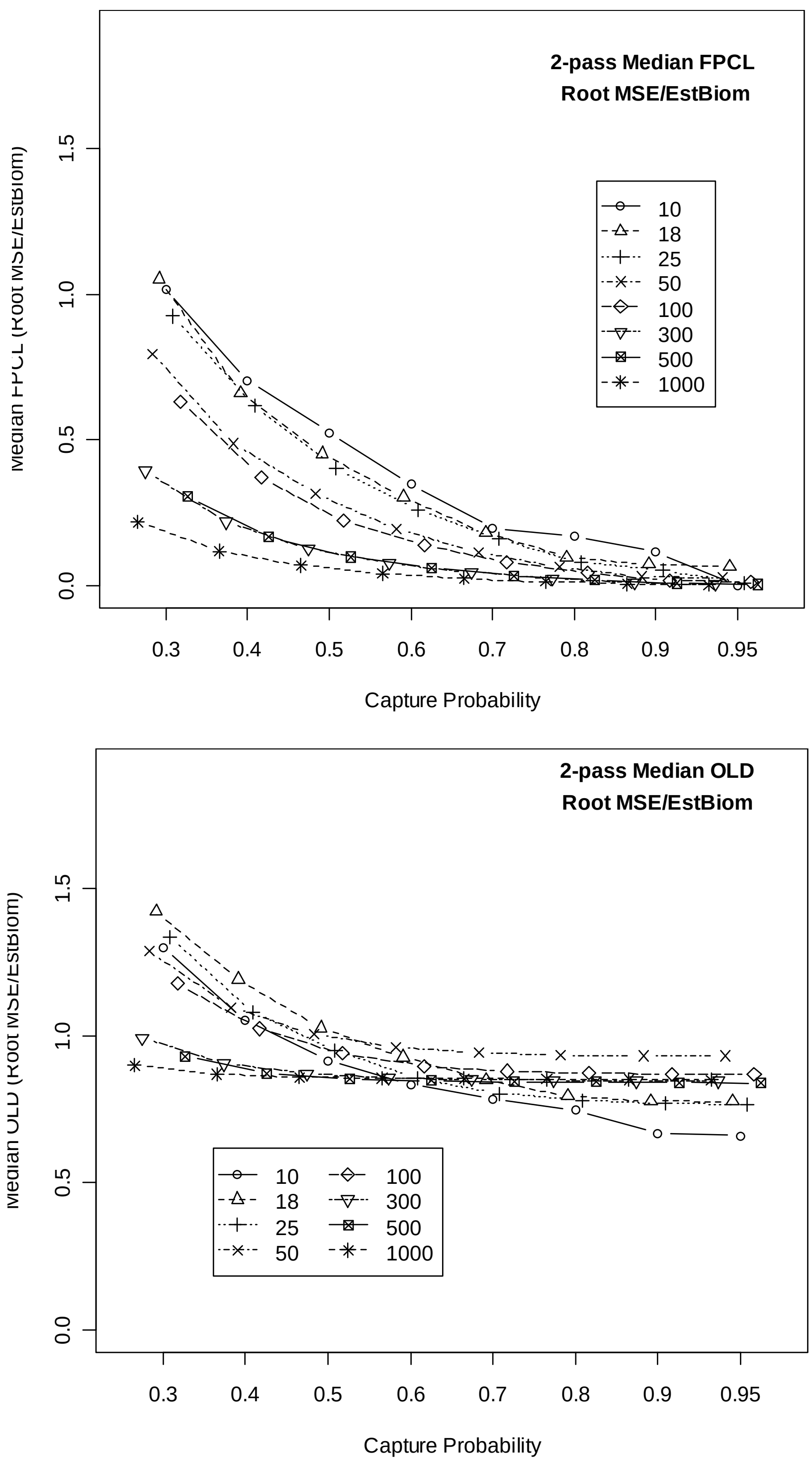


Figure 2.15. Median root-MSE divided by estimated biomass for bias-corrected two-removal estimates of biomass by FPCL (top) and OLD (bottom) methods, true capture probability (x-axis), and true population size (lines).

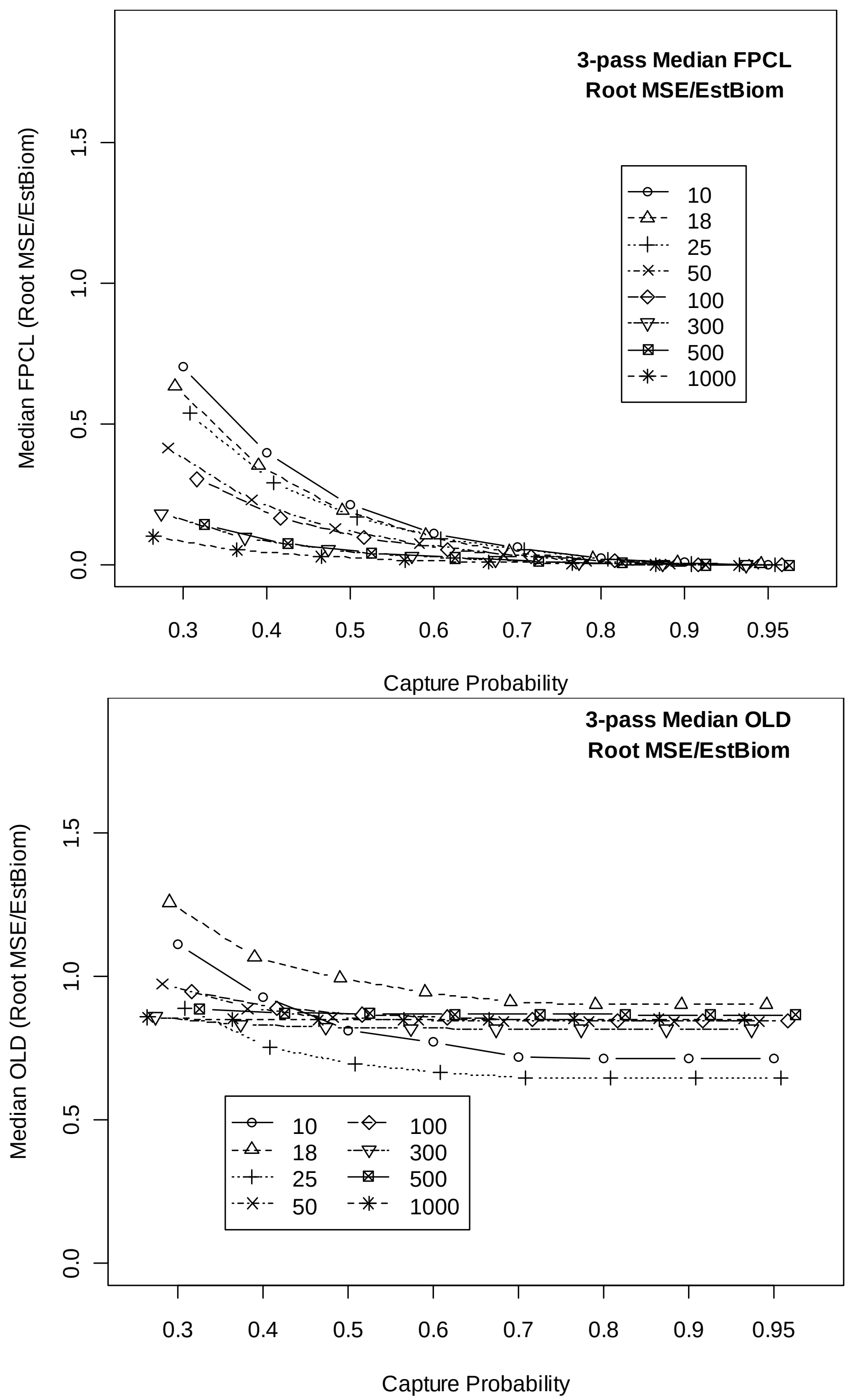


Figure 2.16. Median root-MSE divided by estimated biomass for bias-corrected three-removal estimates of biomass by FPCL (top) and OLD (bottom) methods, true capture probability (x-axis), and true population size (lines).

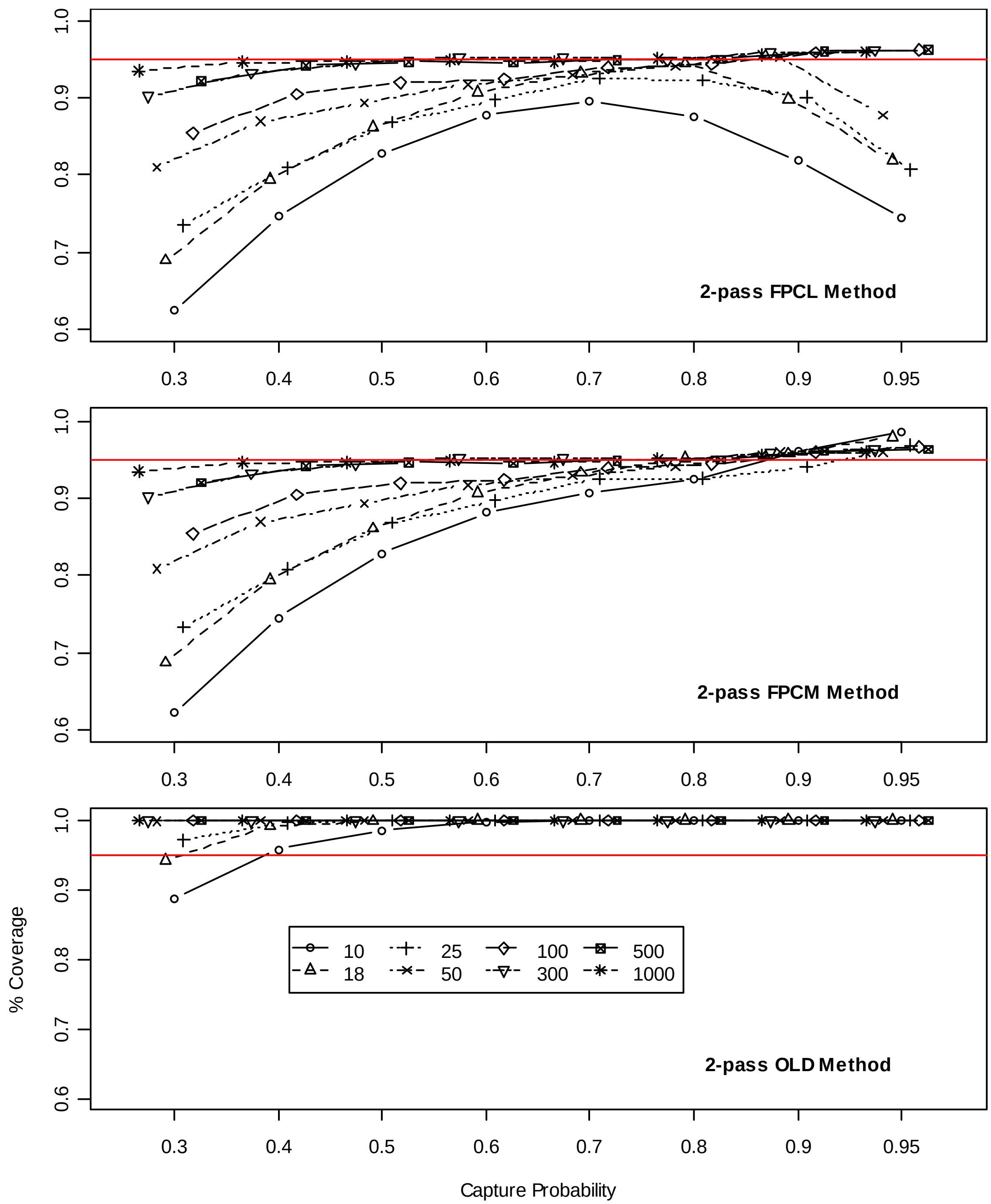


Figure 2.17. Proportion of simulations where the true biomass fell within the 95% confidence intervals for estimates of biomass (% Coverage) for two-pass estimates using the FPCL and OLD methods by true capture probability (x-axis) and true population size (lines). Red lines are the nominal 95% value.

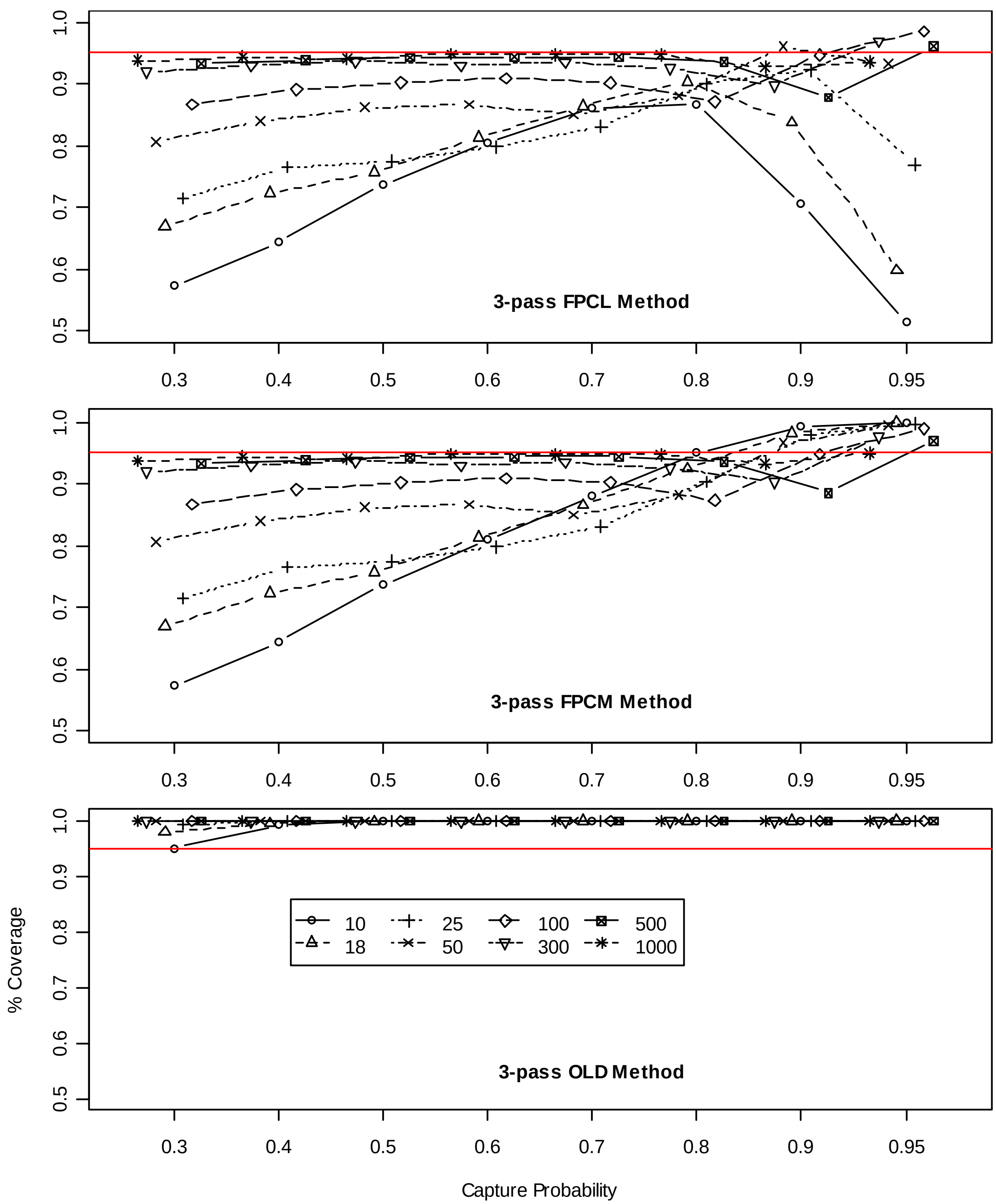


Figure 2.18. Proportion of simulations where the true biomass fell within the 95% confidence intervals for estimates of biomass (% Coverage) for three-pass estimates using the FPCL and OLD methods by true capture probability (x-axis) and true population size (lines). Red lines are the nominal 95% value.

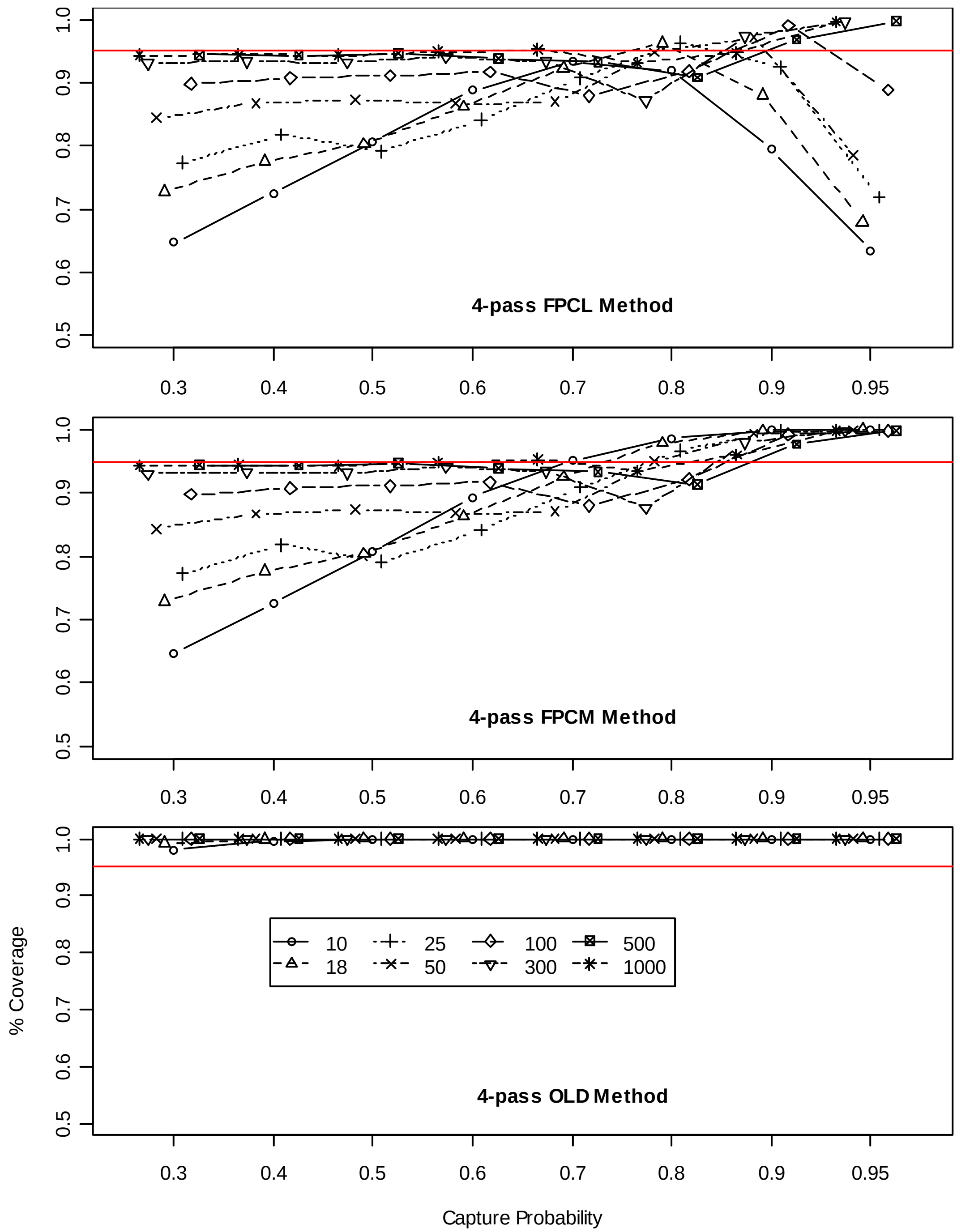


Figure 2.19. Proportion of simulations where the true biomass fell within the 95% confidence intervals for estimates of biomass (% Coverage) for four-pass estimates using the FPCL and OLD methods by true capture probability (x-axis) and true population size (lines). Red lines are the nominal 95% value.

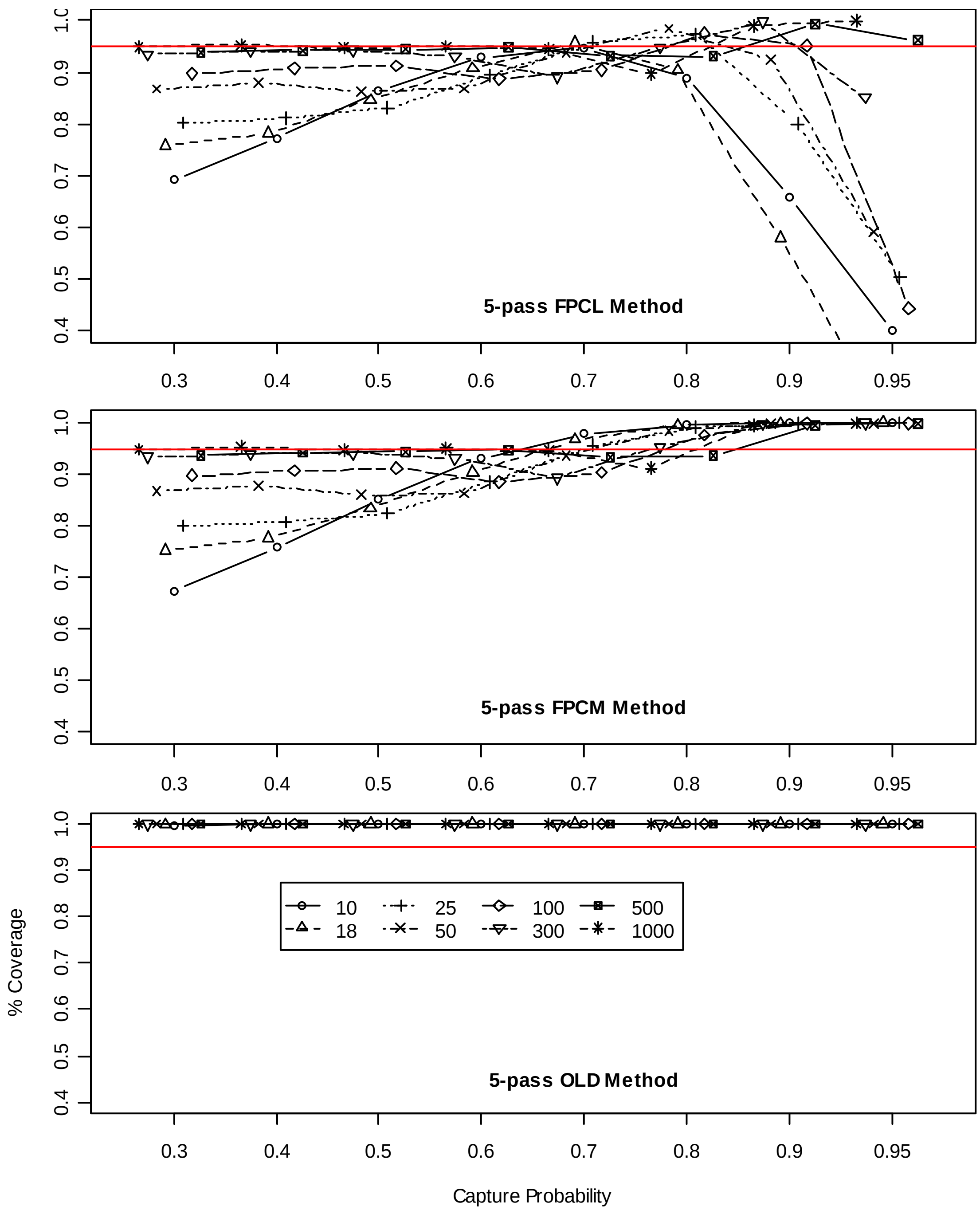


Figure 2.20. Proportion of simulations where the true biomass fell within the 95% confidence intervals for estimates of biomass (% Coverage) for five-pass estimates using the FPCL and OLD methods by true capture probability (x-axis) and true population size (lines). Red lines are the nominal 95% value.

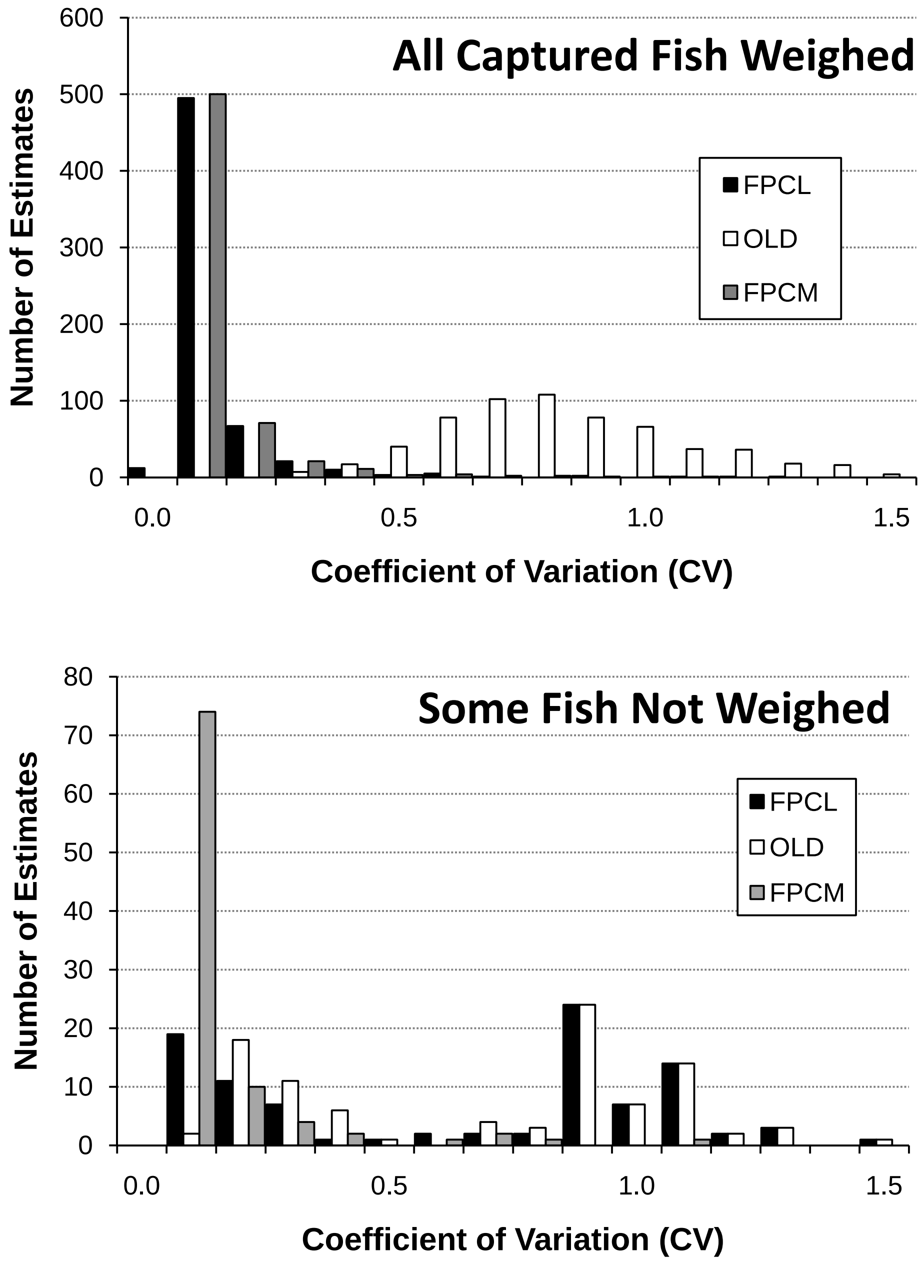


Figure 2.21. Estimated coefficients of variation for field estimates of biomass using traditional (OLD), Lohr (1999) finite population correction factor (FPCL), and model-based finite population correction factor (FPCM) estimators where all captured fish were weighed (top; five CVs >1.5 for OLD not shown) and OLD and FPCM estimators where some captured fish were not weighed (bottom).

CHAPTER 3

REMOVAL OF BROOK TROUT BY ELECTROFISHING TO CONSERVE WESTSLOPE CUTTHROAT TROUT

Abstract

I removed nonnative brook trout, *Salvelinus fontinalis*, by electrofishing from 1.7 to 3.0-km treatment reaches of six streams to conserve sympatric populations of native westslope cutthroat trout, *Oncorhynchus clarkii lewisi*. Brook trout were successfully eliminated from treatment reaches in four of these streams. Eradication success was related to stream size, distribution and abundance of brook trout, years of treatment, number of treatments per year, amounts of instream and riparian cover, cover reduction efforts, and beaver ponds. At least six, and up to eleven, removal treatments of two to four passes per treatment were required to successfully eradicate brook trout. Brook trout were suppressed in two other streams, but dense riparian vegetation, beaver dams, and abundant woody debris in and along the channels prevented eradication. Eradication by electrofishing cost US$3,500 to $5,500 per kilometer where no riparian vegetation or woody debris clearing was necessary, but $8,000 to $9,000 per kilometer where clearing was needed. These treatment costs were similar to estimated costs for using piscicides. Eradication by electrofishing may be preferred where native fish still occur because they can be saved during removal efforts. Use of electrofishing for eradication may be more acceptable to the public than treatment with piscicides and require less time and effort to prepare environmental assessments.

Introduction

Westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) have experienced severe declines in both their distribution and abundance throughout most of their historical range (Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995; Van Eimeren 1996; Shepard et al. 1997, 2003). Factors associated with this decline include introductions of nonnative fishes, habitat changes, and over-exploitation (Hanzel 1959; Liknes and Graham 1988; Behnke 1979, 1992; McIntyre and Rieman 1995). Genetic introgression with introduced rainbow (*O. mykiss*) and Yellowstone cutthroat (*O. c. bouveri*) trout also represents a serious threat to westslope cutthroat trout throughout their range (Allendorf and Leary 1988). Because of the high amount of genetic variability observed among westslope cutthroat trout populations, Allendorf and Leary (1988) recommended the conservation of as many populations throughout the historical range as possible to conserve that genetic diversity.

Westslope cutthroat trout occupy about 59% of their historical habitats in the U.S., and genetically tested populations with no evidence of introgression occupy about 10% (Shepard et al. 2003, 2005). Shepard et al. (1997) estimated that genetically pure populations of westslope cutthroat trout within the upper Missouri basin of Montana occupied less than 5% of their historical range there and indicated that many of the remaining populations had relatively low probabilities of persistence for the next century unless conservation measures were implemented. Montana has a long history of westslope cutthroat trout conservation and formalized a collaborative statewide conservation agreement with federal land management agencies and many private organizations in 1999 that was updated in 2007 (Montana Department of Fish, Wildlife and Parks 1999, 2007). A primary objective of this conservation agreement is the protection and expansion of existing populations.

Many historical habitats formerly occupied by westslope cutthroat trout now contain populations of nonnative trout. In many cases, these nonnative trout have totally replaced westslope cutthroat trout (MacPhee 1966; Griffith 1972; Behnke 1979, 1992; Liknes and Graham 1988; McIntyre and Rieman 1995). This type of replacement has also been suggested for other cutthroat trout subspecies (Behnke 1979 and several papers in Gresswell 1988). A large proportion of historical westslope cutthroat trout habitats in the upper Missouri basin are now occupied by nonnative brook trout, *Salvelinus fontinalis*, introduced during the early 1900s (Figure 1.1; Shepard et al. 1997).

Griffith (1970, 1972) documented dietary overlap between brook trout and westslope cutthroat trout and suggested that brook trout could replace westslope cutthroat trout through competition for food or space or both, but suggested that replacement of cutthroat trout by brook trout probably occurred after habitat degradation had already reduced or eliminated cutthroat trout. Thomas (1996) observed that young brook trout inhibited the foraging efficiency of juvenile Colorado River cutthroat trout, *O. c. pleutiticus*, in a controlled laboratory setting. She suggested that this inhibition might be the mechanism responsible for decreased growth rates of cutthroat trout she documented in the wild. Juvenile brook trout excluded juvenile greenback cutthroat trout *O. c. stomias* from more profitable stream positions (Cummings 1987). When brook trout were physically removed from Whites Creek, a tributary to Canyon Ferry Reservoir in the upper Missouri River of Montana, westslope cutthroat trout abundance increased rapidly, apparently because of increased survival of young, primarily age-0, westslope cutthroat trout (Shepard et al. 2002). A similar response by Colorado River cutthroat trout occurred in four mountain streams in Colorado (Peterson et al. 2004a).

Removal of nonnative fish has been recommended as part of numerous native fish conservation plans (e.g., Cowley 1987; Propst et al. 1992; Langlois et al. 1994; U.S. Fish and Wildlife Service 1993a, 1993b) and is usually accomplished using the piscicides rotenone or antimycin (Davies and Shelton 1983; Marking et al 1983; Meffe 1983; Gresswell 1988; Stevens and Rosenlund 1986; Behnke 1992; Stefferud et al. 1992; Stumpff 1992; Bettoli and Maceina 1996; Hepworth et al. 1999; Knight et al. 1999; Finlayson et al. 2000; Hepworth et al. 2002). However, public concern regarding the use of piscicides (Goodrich and Buskirk 1995; McClay 2000, 2005; Finlayson et al. 2002) and loss of sympatric native fish during treatment with piscicides has focused attention on the potential for using electrofishing to remove unwanted nonnative fish from specific waters. Electrofishing removal of nonnative rainbow trout has been successful in some streams in Great Smoky Mountains National Park (Moore et al. 1986; West et al. 1990); however, Thompson and Rahel (1996) and Meyer et al. (2006) were unsuccessful in removing brook trout from Rocky Mountain streams. I evaluated backpack electrofishing to eradicate brook trout from headwater areas of six Northern Rocky Mountain streams, estimated its costs, provide guidance on types of streams where this technique may be feasible and desirable, and recommend procedures I found most effective.

Study Area

The six study streams were located throughout the upper Missouri River basin in Montana (Figure 3.1). These streams were relatively small, cold, neutral to alkaline, and had low to moderate conductivities (Table 3.1). Elevations and channel gradients of streams and treatment reaches and densities and types of riparian communities varied. Treatment reaches were located in the headwater portions of each stream. Barriers to upstream fish movement were constructed at the lower boundary of each treatment reach. Two barriers were constructed using wooden cribs, one using concrete and rock, two were modified culverts, and one was a modified irrigation diversion. Most barriers had vertical drops of from 1.5 to 3.0 m onto splash pads constructed immediately below each barrier that prevented pools from forming. These barriers prevented upstream invasion by nonnative fish by creating vertical or horizontal water velocity migration barriers, or both, and reducing or eliminating the formation of a pool at downstream end of the barrier from which fish could jump.

Methods

I used electrofishing to remove brook trout and estimate their population abundances using removal estimators (Van Deventer and Platts 1989). Fish were captured using Smith-Root® BP-15, BP-12, and SR-24 backpack electrofishers operated at voltages in the range of 100 to 600 V, frequencies under 50 Hz, and pulse widths less than 2 μsec to maximize the number of fish captured while minimizing injury to fish caused by the shock (Dwyer et al. 2001).

An electrofishing crew consisted of either two or three people. One crewmember wore the backpack shocker and shocked using a wand anode while dragging a cable cathode. A second crewmember was the primary dip netter who followed the shocker netting all stunned fish. When available, a third crewmember held a dip net in the stream channel below the two other crewmembers and carried a mesh bucket for transporting captured fish. Block nets or fencing material (6.5 mm mesh) were installed between sample sections during most sampling and removal events. Two to four electrofishing passes were made during each treatment. All electrofishing passes were generally conducted within four hours, except for one section in Craver Creek, some sections in Muskrat Creek during 2002 and 2003, and in Staubach Creek from 2002 to 2006, where subsequent passes were done the following day. The assumption of population closure was met by 1) using either block fences or nets at the upper and lower ends of all sample sections or, in some cases, locating sections so that shallow riffles or partial velocity barriers were present at their upper and lower boundaries; 2) using a second netter during most sampling to prevent fish from moving downstream; and 3) the relatively short time it took to complete all sample passes (White et al. 1982). The entire length of each treatment reach was usually treated during each removal treatment; however, in some cases I treated less area during later treatments to concentrate removals within those portions of the treatment reach where brook trout predominated and to reduce potential electroshock effects on westslope cutthroat trout (Table 3.2).

Lengths (total length in mm), species, and pass number were recorded for all captured fish. Weights (g) were measured on a relatively large sub-sample of each species, evenly distributed among all lengths of sampled fish, during initial brook trout removal efforts and during at least two of the post-removal sampling efforts. All captured brook trout were removed. Most of these brook trout were marked by removing their adipose fin before moving them below constructed fish barriers to evaluate the effectiveness of these barriers for excluding brook trout.

Brook trout removed during each treatment were classified as age 0, juveniles, or adults based on their lengths. Brook trout less than 100 mm were assumed to be age 0 as judged by length frequency information from these streams and aging of brook trout using otoliths from a similar type of mountain stream in Idaho (Meyer et al. 2006). Brook trout 101 to 149 mm were classified as juveniles and those 150 mm and longer were considered adults.

Abundance estimates of brook trout 75 mm and longer were calculated using removal estimators (Van Deventer and Platts 1989). Removal estimators consistently under-estimate true abundances, especially when only two passes are made and capture probabilities are less than 0.9 (Chapter 2; Riley and Fausch 1992). White et al. (1982) recommended that three or more passes be made unless the capture probability is 0.8 or higher. Three passes reduce estimate bias (Riley and Fausch 1992), but I found that bias is not extreme as long as captured fish comprise at least 70% of the estimated abundance (Chapter 2). Of the 327 removal estimates I made, 223 were two-pass estimates, 92 were three-pass estimates, and 12 required four or more passes to obtain valid estimates. Estimated probabilities of capture were at least 0.7 for 90% and 0.8 or higher for 75% of the two-pass estimates.

Abundances of brook trout 75 mm and longer, and their associated variances, were estimated by sample section and pooled among these sample sections for each treatment period. Abundance estimates and their 95% confidence intervals (CIs) are reported for each treatment period by stream.

Costs of conducting removals were based on $US in 2005 and State of Montana daily per diem rates. I included all costs associated with conducting the removals, but did not include costs of constructing barriers to prevent upstream invasion by nonnative fish nor costs associated with preparing environmental assessments for these projects. Channel and bank clearing costs were included for those projects where they were necessary to accomplish removals. However, channel clearing was not done throughout treatment areas on all such streams.

Results

I considered brook trout to be eradicated from a treatment reach when none were captured during a sampling effort that consisted of at least two electrofishing passes conducted throughout the reach. Eradication was confirmed by subsequent sampling that found no brook trout. I successfully eradicated brook trout from four of the six treatment stream reaches totaling about 10.7 km (Table 3.2). I did not recapture any adipose-clipped brook trout in any treatment reaches above constructed barriers, indicating that the barriers were effective. A few adult brook trout were found above constructed barriers in Whites and Muskrat creeks five to seven years after eradication. These brook trout were again eradicated with two years of moderate removal efforts.

Successful Removals

I successfully eradicated brook trout from Cottonwood, Muskrat, Staubach, and Whites creeks. A single-pass removal of brook trout was made in the lower 0.5-km portion of the treatment reach in Cottonwood Creek in 1998 prior to construction of a fish passage barrier. More intensive brook trout removal efforts began in 2001 after barrier construction. A natural waterfall located about 0.9 km above the constructed barrier was originally believed to have excluded brook trout from the creek above this waterfall, but brook trout were found above it in 2001, and removal efforts there began in 2002. Five removal efforts were needed to eradicate brook trout from the Cottonwood Creek treatment reach. I removed 2,206 brook trout during these efforts. After intensive removal efforts began in 2001, the number of brook trout removed during each treatment declined rapidly (Figure 3.2), as did the estimated numbers of brook trout 75 mm and longer present (Figure 3.4).

I conducted a single removal effort in Muskrat Creek each year from 1997 through 2000, two removal efforts in 2001, four in 2002, and a final one in 2003. Nearly 8,000 brook trout were removed. The number of brook trout captured declined from 1997 through 1999, but the numbers captured and remaining in the treatment reach were nearly constant from 1999 to 2001 (Figures 3.2 and 3.4). Consequently, more removal treatments were done per year in 2001 and 2002 leading to the successful eradication of brook trout in 2004 (Figure 3.4).

Three to four multiple-pass treatments were conducted each year between August and October from 2000 through 2003 in Staubach Creek. About 95% of the total brook trout captured during all removal efforts (1,627) were removed during the initial two treatment years (Figure 3.3). The upper third of the project reach was treated only once per year in 2000 and 2001 to reduce potential electrofishing effects on the small westslope cutthroat trout population. This reduced effort allowed reproduction by brook trout in this upper reach during both years. Multiple treatments conducted throughout the project reach in 2002 and 2003 prevented additional recruitment to the population (Figure 3.5). Brook trout were eradicated by the autumn of 2004, when only one brook trout was captured, and none were found in surveys conducted from 2005 to 2007 (Figure 3.5).

I began brook trout removals in Whites Creek during September 1993 in a 1.4-km treatment reach of the upper stream after installing a temporary fish barrier at its downstream end. I conducted two removal efforts during both 1993 and 1994 in this treatment reach and removed about 400 brook trout (Figure 3.3). A more permanent wooden crib barrier was installed about 1.8 km below the temporary barrier in 1995. A 1.0-km segment of the stream and valley bottom between the upper temporary and lower permanent barriers that had been heavily degraded by past mining activities was also reclaimed in 1995 (Shepard et al. 2002). During reclamation, about 2,750 brook trout were removed from this reclaimed segment by electrofishing from an inflatable raft and subsequent de-watering of the stream channel. In addition, I removed about 1,600 brook trout during two backpack electrofishing removal efforts in about 2.0 km of Whites Creek above the permanent barrier in 1995 (Figure 3.5). I conducted one electrofishing effort annually from 1996 to 2001 above the permanent wooden crib barrier and successfully eradicated brook trout by the end of 2000 (Figure 3.5).

Unsuccessful Removals

I was unable to eradicate brook trout from the treatment reaches of Craver and Spring creeks after three removal efforts, though I removed totals of 494 brook trout from Craver Creek and 541 from Spring Creek. Brook trout populations were suppressed in those sections where repeated removals were completed (Figure 3.6). Dense alder and willow stands, both along and overhanging the channels, and high densities of woody debris within the channels prevented effective electrofishing of large portions of these reaches (Table 3.1). In addition, numerous large beaver ponds in upper Craver Creek supported brook trout, but could not be electrofished. I breached two beaver dams to drain the ponds before attempting to electrofish them. However, electrofishing in these drained ponds was relatively ineffective because deep silt made wading dangerous and created turbidity that made it difficult to see stunned fish.

Costs of Removal Treatments

The total person-days needed to eradicate brook trout from treatment reaches ranged from 70 (23.3days/km) in Cottonwood Creek to 202 (87.8 days/km) in Muskrat Creek. Eradication of brook trout using electrofishing in streams that did not require channel clearing cost about $3,500 to $5,500 per kilometer of stream (Table 3.3). Costs were higher for Muskrat Creek, because of the relative ineffectiveness of annual removal efforts for four years (1997-2000). Where extensive channel clearing was necessary, as in Whites Creek, eradication costs rose to an estimated $8,000 to $9,000 per kilometer.

Discussion

Brook Trout Removals

Brook trout were successfully eradicated from four of the six streams I treated. Eradication success was related to stream size, distribution and abundance of brook trout, years of treatment, number of treatments per year, amounts of instream and riparian cover, cover reduction efforts, and beaver ponds. The efficiency of nonnative fish removal is reduced by increasing stream size, increasing amounts of overhanging and instream cover, the presence of deep pools, and the presence of beaver ponds (Moore et al. 1983, 1986; Habera et al. 1992; Thompson and Rahel 1996).

Capture probabilities of backpack electrofishing for salmonids in streams are negatively related to stream size and amounts of cover, particularly undercut banks and instream woody debris, and positively related to proportion of cobble substrate (Peterson et al. 2004b; Rosenberger and Dunham 2005). Estimated capture probabilities of 1,327 valid depletion abundance estimates I conducted over the past 15 years were usually below 0.7 if wetted widths were six meters or wider. More treatments were required to eradicate brook trout from the treatment reach in Muskrat Creek, which was a moderate-sized headwater stream where brook trout had become well-established throughout the treatment reach, than in the three smaller streams (Table 3.1). Muskrat Creek was steeper than Cottonwood and Whites creeks, but Staubach Creek had the steepest gradient. More effort was required to eradicate brook trout from steeper channel reaches, especially if they contained much woody debris such as was found in Muskrat and Staubach creeks, than from lower gradient reaches (Table 3.1). In contrast, only a few treatments were needed to successfully eliminate brook trout from Cottonwood Creek, a smaller stream with little instream debris where brook trout appeared to have more recently invaded and were not well-established.

The two streams where I was unsuccessful in eradicating brook trout had such dense willow and alder stands and woody debris that it was difficult for crews to even access their channels. Upon access, crews had trouble getting an electrode or dip net into the water in some sections and were often forced to crawl through the channels on their hands and knees. Field crews cleared debris from a small portion of Craver Creek, but only succeeded in clearing about 130 m of the channel in a full day of work. Trimming streamside vegetation and removing in-channel debris from Whites Creek enhanced removal efficiencies and contributed to the successful eradication of brook trout there (Shepard et al. 2002). Elimination of brook trout from Spring Creek by electrofishing might have been possible, but would have required clearing the channel of debris and streamside vegetation. I was able to reduce brook trout to low densities in Staubach Creek after two years of treatments. However, two more years of effort did not eliminate them because abundant woody debris limited removal success in some reaches and I reduced the removal effort in the upper portion of the treatment reach to limit potential electroshock effects on westslope cutthroat trout. Eradication of brook trout from Staubach Creek would probably have occurred earlier had large woody debris been cleared and if I had expended a consistent high level of effort throughout the treatment reach. Overhanging vegetation and the presence of woody debris reduced capture probabilities of age-0 brook trout from a Wyoming stream (Thompson and Rahel 1996).

Removal efforts were hindered in Craver Creek by numerous large beaver ponds in its upper reaches. These ponds served as refuges for brook trout because I could not effectively remove brook trout from them. Even after some of these ponds were drained, deep silt that had accumulated in these ponds made wading extremely dangerous and turbidity stirred up by wading made it difficult to see shocked fish. Similar difficulties were encountered in Wyoming (Thompson and Rahel 1996); about 70% of age-0 brook trout in upper LaBarge Creek were concentrated in a single beaver pond (Thompson 1995). Chemical treatment is probably the only viable alternative for eradicating brook trout from upper Craver Creek, but it would also require at least partial draining of the beaver ponds. In LaBarge Creek, brook trout were eventually removed using piscicides from 1999 through 2007 (http://gf.state.wy.us/services/news/pressreleases/07/10/06/071006_1.asp).

At least six and up to ten multiple-pass electrofishing removal efforts (two or more passes per effort) were necessary to eradicate brook trout from small to medium-sized streams (Table 3.2). It was more effective to concentrate removal efforts within a one to three-year time period than to conduct single annual removal efforts over five or more years. I was unable to eradicate, or even effectively reduce, brook trout from Muskrat Creek until I began conducting multiple removal treatments each year, suggesting that this might be the only viable treatment strategy for moderate-sized streams (Table 3.2). Repeated, intensive electrofishing removals conducted over time reduced or eradicated nonnative rainbow trout in streams of Great Smoky Mountains National Park (Moore et al. 1983, 1986; Larson et al. 1986) and condensing removal efforts over a one to two-year period was found to be most effective (Kulp and Moore 2000). Brook trout abundances were substantially reduced, but not eradicated, by three electrofishing passes conducted once in each of three Wyoming streams (Thompson and Rahel 1996). An additional one-pass electrofishing effort conducted in these streams the following year helped to further reduce brook trout numbers, especially of age-1 fish that were missed when they were age 0 the previous year. Removal of brook trout from an Idaho stream by electrofishing slightly reduced their abundances, but did not change annual survival rates, probably as a function of density dependent compensatory mechanisms (Meyer et al. 2006). However, only three separate four-pass removal efforts, one per year for three years, were conducted. Based on my experience, either continuation of single annual removal efforts for six or seven years or four to six removal efforts condensed into two or three years might have successfully eradicated brook trout from the treatment reach of this Idaho stream, given the relatively high estimated capture probabilities (> 0.8) for age-1 and older brook trout (Meyer et al. 2006).

Cost of Removals

Meyer et al. (2006) spent a total of 217 person-days in an unsuccessful attempt to eradicate brook trout from 7.8 km of a stream in Idaho (27.8 days/km), while I spent 70 to 202 days (23.3 to 87.8 days/km) to successfully eradicate them from three stream reaches. I compared my electrofishing eradication costs to similar projects in Montana that used piscicides (either antimycin or rotenone) from 1999 through 2008. My costs of electrofishing removal where no channel clearing was necessary ($3,500 to $5,500 per km) were lower than estimated costs of two antimycin treatments (about $5,000 to $7,000 per km) and higher than those of two rotenone treatments (about $3,000 to $5,000 per km; Pat Clancey, Dave Moser, and Lee Nelson, personal communications). Costs of electrofishing removals almost doubled where channel clearing was needed ($8,000/km). These costs do not include the environmental assessments and public involvement that must precede eradication treatments using either electrofishing or piscicides. Eradication by piscicides would probably require greater levels of environmental assessment and public involvement than electrofishing treatments (Finlayson et al. 2000); thus, treatment costs for piscicides may be similar or higher than costs of electrofishing removals if environmental assessment and public involvement costs are included.

Removal of nonnative trout using electrofishing appears to be a viable alternative to using piscicides, especially in smaller streams where extant populations of native trout are sympatric with nonnative fish because electrofishing allows for the collection and preservation of the native trout during removal of nonnative fish. Even when an attempt is made to salvage native species prior to treatment with piscicides, it is usually possible to save only a low to moderate proportion of the native population and holding these salvaged fish increases costs and project complexity. However, treatments with piscicides may be the only viable alternative for larger streams (base discharge wetted widths > 6 m), or where dense stands of woody vegetation or beaver ponds make electrofishing difficult or impossible. In streams that are four to six meters wide electrofishing eradication should be possible, but simultaneous electrofishing by two crews will probably be necessary. This increased effort will increase the cost.

Need for Barriers

A barrier to upstream fish movement at the lower boundary of any removal project is necessary to ensure nonnative species do not move upstream to re-colonize reclaimed habitats (Moore et al. 1983; Hepworth et al. 2001; Shepard et al. 2002; Peterson et al. 2004a). Existing cutthroat trout recovery plans have recognized the importance of barriers to prevent competition and hybridization with nonnative trout species (U.S. Fish and Wildlife Service 1993a, 1993b; Langlois et al. 1994). Natural waterfalls are ideal barriers, and they should be used where available. However, where no waterfalls exist, barriers will need to be constructed. Many greenback cutthroat trout restoration attempts failed because of competition with nonnative salmonids (Harig et al. 2000). Many of these failures were caused by incomplete removal efforts, but in some cases re-invasion over man-made barriers had occurred. Man-made barriers are not as effective as natural waterfalls (Harig et al. 2000) and humans might move nonnative fish over barriers (Harig et al. 2000), something I believe may have occurred at two of my treatment sites (Whites and Muskrat creeks) where barriers were located immediately adjacent to public roads and a few adult brook trout were found above the barriers five to seven years after eradication had occurred.

Recommendations

1. A thorough basin-wide fish survey must be done before conducting electrofishing removals to confirm the distribution of fish throughout the proposed treatment area.
2. A barrier to upstream fish movement should be installed at the lower boundary of the treatment area.
3. Where stream channels have dense riparian cover along and over the channel, high amounts of woody debris within the channel, or both, plan to remove or clear this vegetation and debris prior to beginning electrofishing treatments to allow better access to the stream channel and enhance electrofishing efficiency.
4. Consider treating relatively long sections where a single electrofishing pass can be conducted in one day and then make subsequent electrofishing passes on subsequent days. This procedure prevents crew "burn-out" and often increases capture probability.
5. At least six treatments of two to three passes per treatment should be planned. Eradication of the target species should be the goal. Suppression (i.e., not eradication) of nonnative trout populations can be accomplished with repeated electrofishing removals, but the permanent effort and expense required make it a poor long-term conservation strategy. Suppression of nonnative fish populations can be used to provide short-term relief to a native fish population at imminent risk of extinction until a long-term solution can be implemented.

6. Several removal treatments should be conducted during the first year.
7. At least three passes per treatment should be made during initial treatments and then at least two passes per treatment should be made until few individuals of the target species are captured.
8. Remove as many reproductive adults as possible prior to the spawning season (i.e., prior to September for brook trout; Figures 3.2 through 3.5) during the initial year of treatments using at least three removal passes per treatment. Juvenile fish can be eradicated during subsequent years when they are larger and easier to shock, see, and net.
9. Conduct some electrofishing treatments during the spawning season of the nonnative fish species to take advantage of the aggregating behavior of adults.
10. Avoid electrofishing over spawning areas used by native fish when their eggs are incubating, but plan to shock over and physically trample spawning areas used by the target nonnative fish species immediately after they have spawned. Trampling and electrofishing over trout redds reduces embryo survival (Roberts and White 1992; Dwyer et al. 1993). I used this strategy sporadically in Muskrat Creek, but did not quantitatively evaluate it.
11. Conduct at least one treatment per year late in the fall to take advantage of fish aggregations in over-wintering pools (Bustard and Narver 1975; Cunjak and Power 1986; Brown and Mackay 1995; Jakober et al. 1998; Muhlfeld et al. 2001; Roni and Quinn 2001; Dare and Hubert 2002) and the larger sizes that juvenile, particularly age-0, brook trout attain following a full summer of growth, which

make them more vulnerable to electrofishing (Thompson and Rahel 1996). Cooler water temperatures I encountered during fall treatments (~ 4˚C) made electrofishing more efficient than I experienced during the heat of the summer when water temperatures were 15˚C or higher.

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Literature Cited

Allendorf, F. W., and R. F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. Conservation Biology 2:170-184.

Behnke, R. J. 1979. Monograph of the native trouts of the genus *Salmo* of western North America. Report of R. J. Behnke to U.S. Department of Interior Bureau of Land Management and Fish and Wildlife Service, and Department of Agriculture Forest Service, Region 2, Lakewood, Colorado.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Bettoli, P. W., and M. J. Maceina. 1996. Sampling with toxicants. Pages 303-330 *in* B. R. Murphy and P. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Brown, R. S., and W. C. Mackay. 1995. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. Transactions of the American Fisheries Society 124:873-885.

Bustard, D. R., and D. W. Narver. 1975. Preferences of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Salmo clarki*) relative to simulated alteration of winter habitat. Journal of the Fisheries Research Board of Canada 32:681-687.

Cowley, P. C. 1987. Potential for increasing abundance of cutthroat in streams by stocking fry and removal of brook trout. Master's thesis. University of Idaho, Moscow.

Cummings, T. R. 1987. Brook trout competition with greenback cutthroat trout in Hidden Valley Creek, Colorado. Master’s thesis. Colorado State University, Fort Collins.

Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 43:1970-1981.

Dare, M. R., and W. A. Hubert. 2002. Changes in habitat availability and habitat use and movements by two trout species in response to declining discharge in a regulated river during winter. North American Journal of Fisheries Management 22:917-928.

Davies, W. D., and W. L. Shelton. 1983. Sampling with toxicants. Pages 199-213 *in* L. A. Nielson and D. L. Johnson, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Dwyer, W. P., B. B. Shepard, and R. G. White. 2001. Effect of backpack electroshock on westslope cutthroat trout injury and growth 110 and 250 days posttreatment. North American Journal of Fisheries Management 21:646-650.

Dwyer, W. P., W. Fredenberg, and D. A. Erdahl. 1993. Influence of electroshock and mechanical shock on survival of trout eggs. North American Journal of Fisheries Management 13:839-843.

Finlayson, B. J., R. A. Schnick, R. L. Cailteux, L. DeMong, W. D. Horton, W. McClay, C. W. Thompson, and G. J. Tichacek. 2000. Rotenone use in fisheries management: administrative and technical guidelines manual. American Fisheries Society, Bethesda, Maryland.

Finlayson, B. J., R. A. Schnick, R. L. Cailteux, L. DeMong, W. D. Horton, W. McClay, and C. W. Thompson. 2002. Assessment of antimycin A use in fisheries and its potential for re-registration. Fisheries 27(6):10-18.

Goodrich, J. M., and S. W. Buskirk. 1995. Control of abundant native vertebrates for conservation of endangered species. Conservation Biology 9:1357-1364.

Gresswell, R. E. 1988. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.

Griffith, J. S., Jr. 1970. Interaction of brook trout and cutthroat trout in small streams. Doctoral dissertation. University of Idaho, Moscow.

Griffith, J. S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki)* in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada 29:265-273.

Habera, J. W., R. J. Strange, and S. E. Moore. 1992. Stream morphology affects trout capture efficiency of an AC backpack electrofisher. Journal of the Tennessee Academy of Science 67:55-58.

Hanzel, D. A. 1959. The distribution of the cutthroat trout (*Salmo clarki*) in Montana. Proceedings of the Montana Academy of Sciences 19:32-71.

Harig, A. L., K. D. Fausch, and M. K. Young. 2000. Factors influencing success of greenback cutthroat trout translocations. North American Journal of Fisheries Management 20:994-1004.

Hepwerth, D. K., M. J. Otterbacher, and C. B. Chamberlain. 2002. A review of a quarter century of native trout conservation in southern Utah. Intermountain Journal of Sciences 8:125-142.

Hepworth, D. K., M. J. Ottenbacher, and C. B. Chamberlain. 2001. Occurrence of native Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in the Escalante River drainage, Utah. Western North American Naturalist 61:129-138.

Hepworth, D. K., M. J. Ottenbacher, and J. E. Whelan. 1999. Restoration of native Bonneville cutthroat trout in the North Fork North Creek, Beaver County, Utah. Utah Division of Wildlife Resources, Salt Lake City.

Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127:223-235.

Knight, C. A., R. W. Orme, and D. A. Beauchamp. 1999. Growth, survival, and migration patterns of juvenile adfluvial Bonneville cutthroat trout in tributaries of Strawberry Reservoir, Utah. Transactions of the American Fisheries Society 128:553-563.

Kulp, M. A., and S. E. Moore. 2000. Multiple electrofishing removals for eliminating rainbow trout in a small southern Appalachian stream. North American Journal of Fisheries Management 20:259-266.

Langlois, D., J. Cameron, D. Smith, M. Japhet, C. S. Hutchinson, and J. Castellano. 1994. Colorado River cutthroat trout conservation strategy for southwestern Colorado. Colorado Division of Wildlife and U.S. Department of Agriculture, Forest Service, Montrose.

Larson, G. L., S. E. Moore, and D. C. Lee. 1986. Angling and electrofishing for removing nonnative rainbow trout from a stream in a national park. North American Journal of Fisheries Management 6:580-585.

Liknes, G. A., and P. J. Graham. 1988. Westslope cutthroat trout in Montana: life history, status and management. American Fisheries Society Symposium 4:53-60.

MacPhee, C. 1966. Influence of differential angling mortality and stream gradient on fish abundance in a trout-sculpin biotope. Transactions of the American Fisheries Society 95:381-387.

Marking, L. L., T. D. Bills, J. J. Rach, and S. J. Grabowski. 1983. Chemical control of fish and fish eggs in the Garrison Diversion Unit, North Dakota. North American Journal of Fisheries Management 3:410-418.

McClay, W. 2000. Rotenone use in North America (1988-1997). Fisheries 25(5):15-21.

McClay, W. 2005. Rotenone use in North America (1988-2002). Fisheries 30(4):29-31.

McIntyre, J. D., and B. E. Rieman. 1995. Westslope cutthroat trout. Pages 1-15 *in* M. K. Young, editor. Conservation assessment for inland cutthroat trout. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-256, Fort Collins, Colorado.

Meffe, G. K. 1983. Attempted chemical renovation of an Arizona springbrook for management of the endangered Sonoran topminnow. North American Journal of Fisheries Management 3:315-321.

Meyer, K. A., J. A. Lamansky, and D. J. Schill. 2006. Evaluation of an unsuccessful brook trout electrofishing removal project in a small Rocky Mountain stream. North American Journal of Fisheries Management 26:849-860.

Montana Department of Fish, Wildlife and Parks. 1999. Memorandum of understanding and conservation agreement for westslope cutthroat trout (*Oncorhynchus clarki lewisi*) in Montana, Helena.

Montana Department of Fish, Wildlife and Parks. 2007. Memorandum of understanding and conservation agreement for westslope cutthroat trout and Yellowstone cutthroat trout in Montana, Helena.

Moore, S. E., B. Ridley, and G. L. Larson. 1983. Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. North American Journal of Fisheries Management 3:72-80.

Moore, S. E., G. L. Larson, and B. L. Ridley. 1986. Population control of exotic rainbow trout in streams of a natural area park. Environmental Management 10:215-219.

Muhlfeld, C. C., D. H. Bennett, and B. Marotz. 2001. Fall and winter habitat use and movement by Columbia River redband trout in a small stream in Montana. North American Journal of Fisheries Management 21:170-177.

Peterson, D. P., K. D. Fausch, and G. C. White. 2004a. Population ecology of an invasion: effects of brook trout on native cutthroat trout. Ecological Applications 14:754-772.

Peterson, J. T., R. F. Thurow, and J. W. Guzevich. 2004b. An evaluation of multipass electrofishing for estimating the abundance of stream-dwelling salmonids. Transactions of the American Fisheries Society 133:462-475.

Propst, D. L., J. A. Stefferud, and P. R. Turner. 1992. Conservation and status of Gila trout, *Oncorhynchus gilae*. The Southwestern Naturalist 37:117-125.

Riley, S. C., and K. D. Fausch. 1992. Underestimation of trout population size by maximum-likelihood removal estimates in small streams. North American Journal of Fisheries Management 12:768-776.

Roberts, B. C., and R. G. White. 1992. Effects of angler wading on survival of trout eggs and pre-emergent fry. North American Journal of Fisheries Management 12:450-459.

Roni, P., and T. P. Quinn. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58:282-292.

Rosenberger, A. E. and J. B. Dunham. 2005. Validation of abundance estimates from mark-recapture and removal techniques for rainbow trout captured by electrofishing in small streams. North American Journal of Fisheries Management 25:1395-1410.

Shepard, B. B., B. E. May, and W. Urie. 2003. Status of westslope cutthroat trout (*Oncorhynchus clarki lewisi*) in the United States: 2002. Report of the Westslope Cutthroat Trout Interagency Conservation Team to Montana Fish, Wildlife and Parks, Helena.

Shepard, B. B., B. E. May, and W. Urie. 2005. Status and conservation of westslope cutthroat trout within the western United States. North American Journal of Fisheries Management 25:1426-1440.

Shepard, B. B., B. Sanborn, L. Ulmer, and D. C. Lee. 1997. Status and risk of extinction for westslope cutthroat trout in the upper Missouri River basin. North American Journal of Fisheries Management 17:1158-1172.

Shepard, B. B., R. Spoon, and L. Nelson. 2002. A native westslope cutthroat trout population responds positively after brook trout removal and habitat restoration. Intermountain Journal of Sciences 8:193-214.

Stefferud, J. A., D. L. Propst, and G. L. Burton. 1992. Use of antimycin to remove rainbow trout from White Creek, New Mexico. Pages 55-56 in D. A. Hendrickson, editor. Proceedings of the Desert Fishes Council, Bishop, California.

Stevens, D. R., and B. D. Rosenlund. 1986. Greenback cutthroat trout restoration in Rocky Mountain National Park. Pages 104-118 *in* G. Larson and M. Soukup, editors. Proceedings of the Conference on Science in the National Parks, Volume 6: Fisheries and Coastal Wetlands Research, U.S. National Park Service and The George Wright Society, Hancock, Michigan.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union 38:913-920.

Stumpff, W. K. 1992. Stabilization of native trout populations. Federal Aid in Fish Restoration, Project F-22-R-33, Number 302, New Mexico Department of Game and Fish, Albuquerque.

Thomas, H. M. 1996. Competitive interactions between a native and exotic trout species in high mountain streams. Master's thesis. Utah State University, Logan.

Thompson, P.D. 1995. Evaluating the effectiveness of electrofishing and man-made barriers for controlling brook trout populations in streams containing cutthroat trout. Master's thesis. University of Wyoming, Laramie.

Thompson, P. D., and F. J. Rahel. 1996. Evaluation of depletion-removal electrofishing of brook trout in small Rocky Mountain streams. North American Journal of Fisheries Management 16:332-339.

U.S. Fish and Wildlife Service. 1993a. Gila Trout Recovery Plan. U.S. Department of Interior, Albuquerque, New Mexico.

U.S. Fish and Wildlife Service. 1993b. Greenback Cutthroat Trout Recovery Plan. U.S. Department of Interior, Denver, Colorado.

Van Deventer, J. S., and W. S. Platts. 1989. Microcomputer software system for generating population statistics from electrofishing data - User's guide for Microfish 3.0. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, General Technical Report INT-254, Ogden, Utah.

Van Eimeren, P. 1996. Westslope cutthroat trout *Oncorhynchus clarki lewisi*. Pages 1-10 *in* D.A. Duff, technical editor. Conservation assessment for inland cutthroat trout distribution, status and habitat: Management implications. U.S. Department of Agriculture, Forest Service, Intermountain Region, Ogden, Utah.

West, J. L., S. E. Moore, and M. R. Turner. 1990. Evaluation of electrofishing as a management technique for restoring brook trout in Great Smoky Mountains National Park. U.S. Department of Interior, Research/Resources Management Report SER-09/01, Gatlinburg, Tennessee.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. U.S. Department of Energy, Los Alamos National Laboratory, Report number: LA-8787-NERP, Los Alamos, New Mexico.

Table 3.1. Physical characteristics of six Rocky Mountain streams where brook trout removals were conducted from 1993 through 2004.

	Stream					
Parameter	Cottonwood	Craver	Muskrat	Spring	Staubach	Whites
Elevation range of entire stream (m)	970-1830	2200-2800	1480-2350	1470-2320	1500-1840	1200-1870
Elevation range of treatment reach (m)	1590-1780	2300-2400	1920-2110	1880-2120	1500-1730	1600-1790
Length of stream (km)	31.1	5.8	33.9	24.0	11.4	25.5
Treatment length (km)	3.0	2.8	2.4	1.7	2.5	2.9
Wetted width (m)	2.4	1.2	2.6	1.7	1.6	2.0
Channel order[1]	3rd	2nd	3rd	3rd	2nd	3rd
Channel gradient (%)	6	3	6	5	11	3
Riparian vegetation (density and predominant types)	Sparse willow, aspen	Dense willow, alder	Moderate conifer, alder	Dense willow, alder	Moderate conifer, alder	Moderate to dense willow, alder[2]
Late summer discharge (m^3/sec)	0.10	0.05	0.17	0.07	0.06	0.08
Summer water temperature (°C)	12-17	5-20	6-16	9-20	10-19	8-10
Conductivity (μmhos)	88	44	72	230	60	660
pH	8.7	8.2	8.4	8.9	7.9	8.2

[1] Strahler (1957) stream order classification.

[2] Areas of dense riparian vegetation along and within Whites Creek were cleared prior to conducting removal efforts.

Table 3.2. Number of treatments, distance treated, number of removal passes, and number of brook trout removed by year and stream during brook trout removal efforts conducted in Cottonwood, Craver, Muskrat, Spring, Staubach, and Whites creeks from 1993 through 2005. Total treatments, passes, and number of brook removed during brook trout eradication are shown. If no brook trout were captured during two consecutive removal efforts in a portion of a treatment reach, subsequent efforts did not include that portion of the reach; distances treated therefore usually declined over time.

Stream Year	Number of times treated	Distance (km) treated	Total number of passes	Brook trout removed
Cottonwood Creek				
1998	1	0.5	1	494
2001	2	1.6	4	1574
2002	2	3	5	130
2003	2	2.3	3	8
2004	1	2.3	2	0
2005	1	1.6	1	0
Total	**7**		**13**	**2206**
Craver Creek				
2001	2	2.6	4	469
2002	1	0.9	2	25
Total	**3**		**6**	**494**
Muskrat Creek				
1997	1	2.4	2	1933
1998	1	2.4	2	1443
1999	1	2.4	2	1090
2000	1	2.4	3	1095
2001	2	2.4	5	1768
2002	5	2.4	10	589
2003	2	2.4	5	18
2004	1	2.4	2	0
2005	1	0.7	2	0
Total	**13**		**29**	**7936**

Table 3.2. Continued.

Stream Year	Number of times treated	Distance (km) treated	Total number of passes	Brook trout removed
Spring Creek				
2001	2	1.3	5	455
2002	1	1	2	86
Total	**3**		**7**	**541**
Staubach Creek				
2000	3	2.5	7	1394
2001	4	2.5	12	146
2002	3	2.5	6	70
2003	3	2.5	6	16
2004	1	2.5	2	1
2005	1	2	2	0
2006	1	2.5	2	0
Total	**14**		**24**	**1627**
Whites Creek				
1993	1	1.4	2	111
1994	1	1.1	2	33
1995	1	3	3	4271
1996	1	1.9	2	144
1997	1	2.1	2	135
1998	1	2.8	2	238
1999	1	2.7	3	91
2000	1	1.8	3	4
2001	1	1.8	2	0
2002	1	0.5	2	0
Total	**8**		**19**	**5027**

Table 3.3. Costs ($US in 2005) to successfully eradicate brook trout from the headwater portions of four Northern Rocky Mountain streams

Item	Cottonwood	Muskrat	Staubach	Whites
Personnel on site	$6,400.00	$17,100.00	$10,000.00	$9,500.00
Personnel travel time	$600.00	$3,100.00	$0.00	$1,000.00
Per diem	$2,304.00	$6,156.00	$600.00	$1,800.00
Mileage	$875.00	$630.00	$616.00	$1,085.00
Supplies	$400.00	$775.00	$2,500.00	$2,375.00
Channel clearing	$0.00	$0.00	$0.00	$7,500.00
Total	**$10,579.00**	**$27,761.00**	**$13,716.00**	**$23,260.00**
Kilometers treated	3.0	2.4	2.5	2.9
Cost per km	$3,527.00	$11,567.00	$5,486.40	$8,020.00

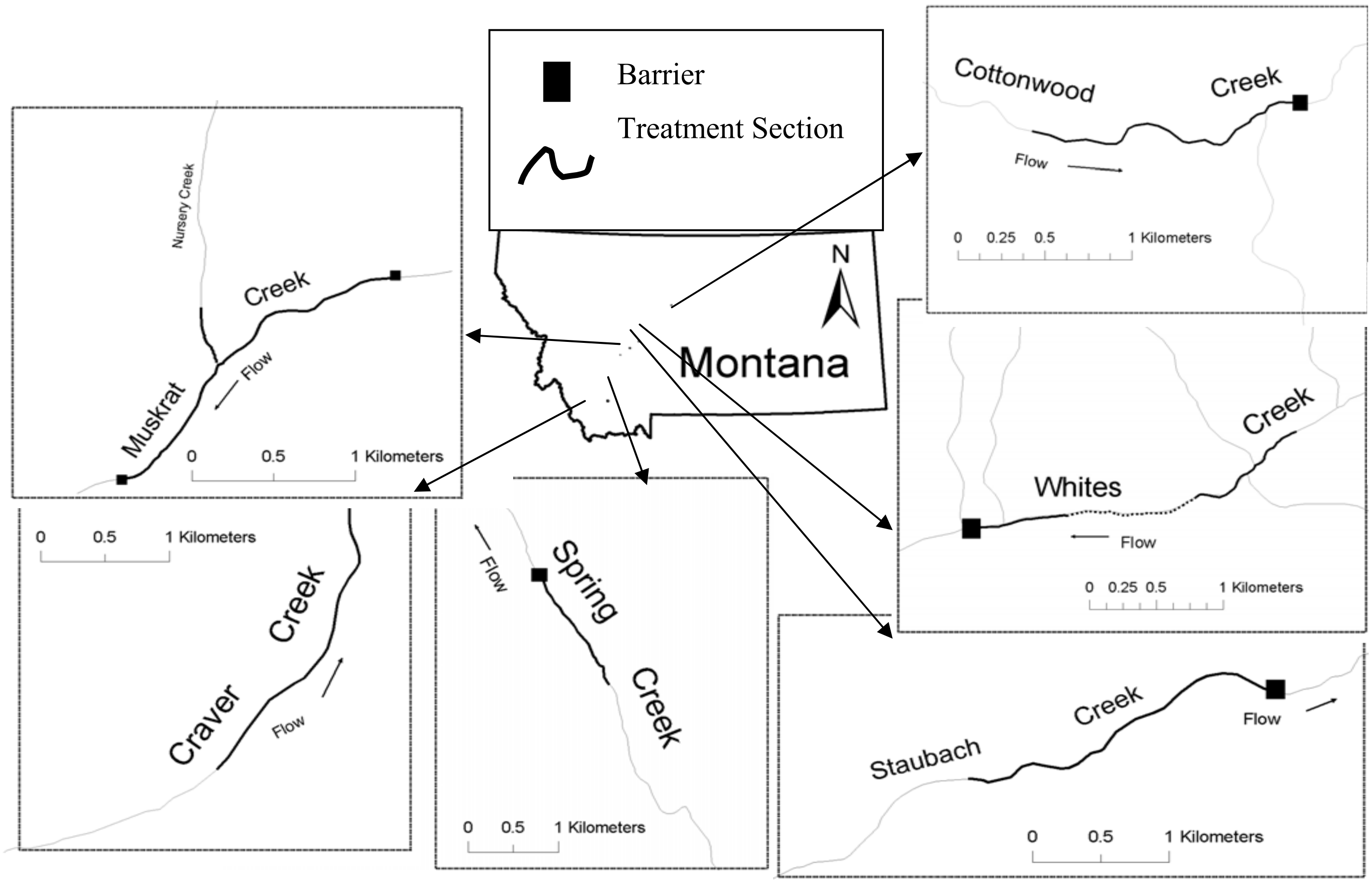

Figure 3.1. Locations of streams and treatment reaches where brook trout were removed by electrofishing to conserve westslope cutthroat trout. Brook trout were removed by dewatering a segment of Whites Creek (dashed bold line between the two continuous bold treatment lines) during a mining reclamation project in 1995 (see Shepard et al. 2002).

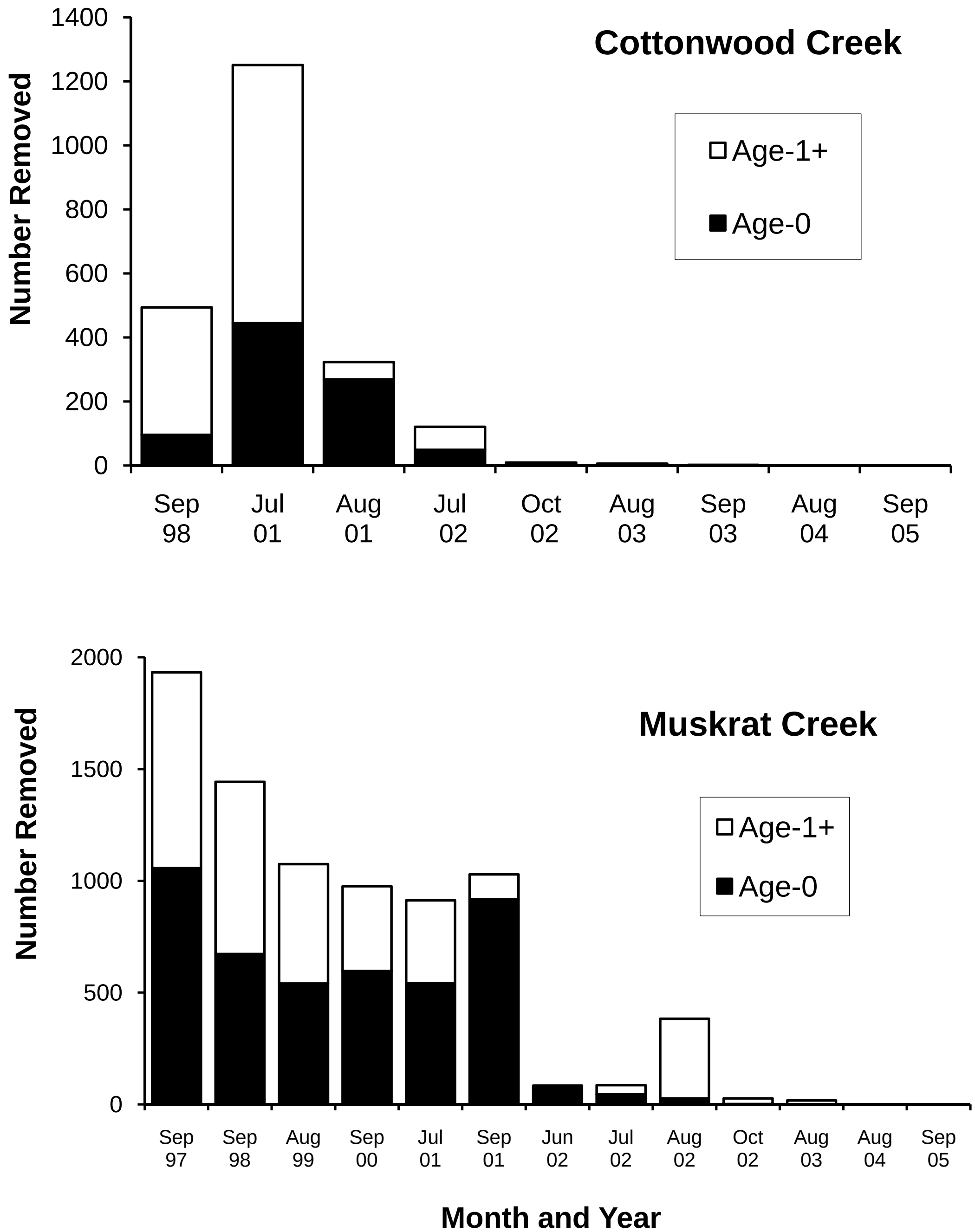

Figure 3.2. Number of age-0 and age-1 and older (Age-1+) brook trout removed by electrofishing during each time period (month and year) in the treatment reaches of Cottonwood and Muskrat creeks. Only a partial removal was done in Cottonwood Creek in1998.

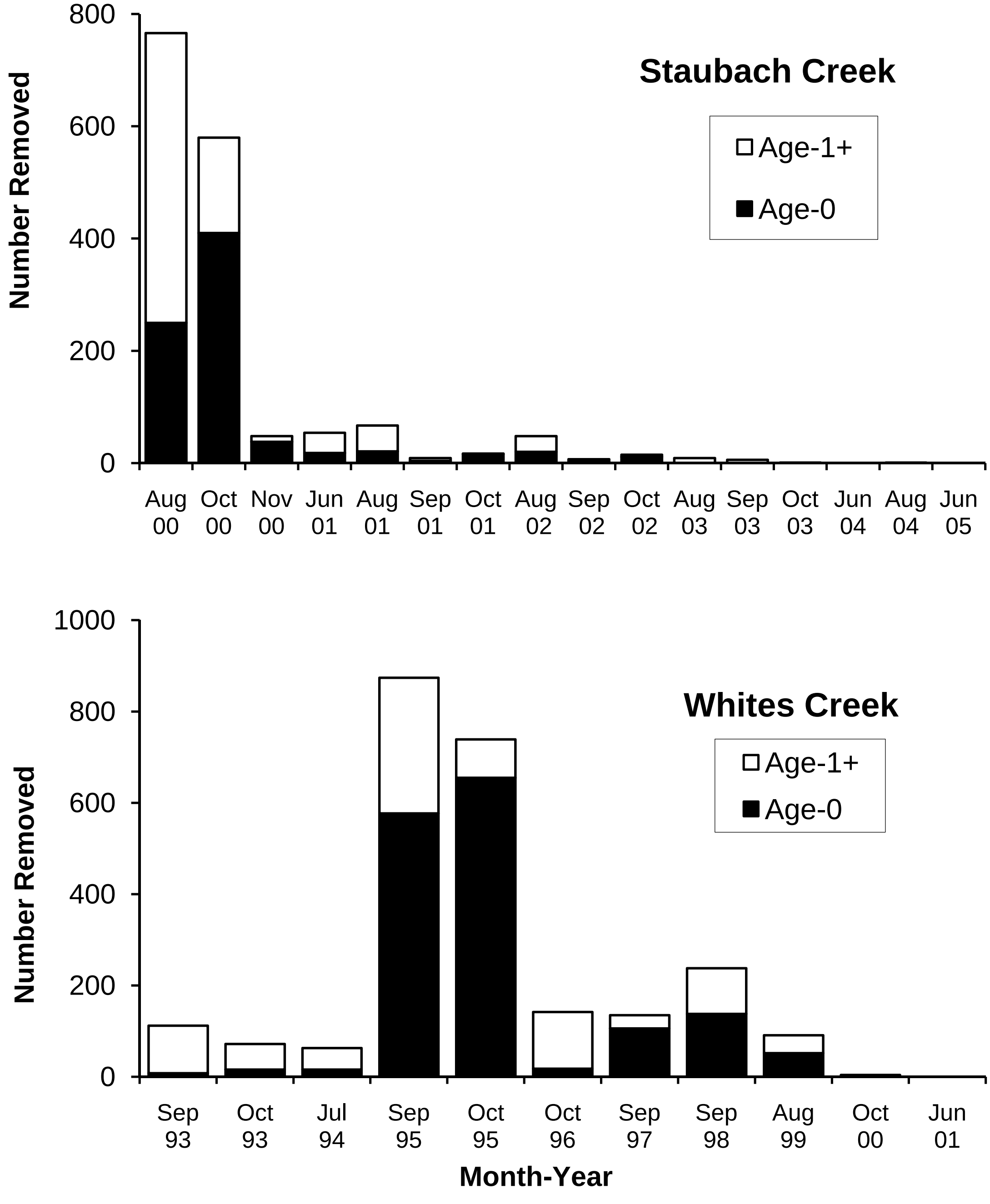

Figure 3.3 Number of age-0 and age-1 and older (Age-1+) brook trout removed by electrofishing during each time period (month and year) in the treatment reaches of Staubach and Whites creeks. Removals were only done in the upper half of the treatment section of Whites Creek in 1993 and 1994 and about 2,750 brook trout removed from old mining settling ponds in the lower half of the treatment reach during their reclamation in 1995 are not included in this figure.

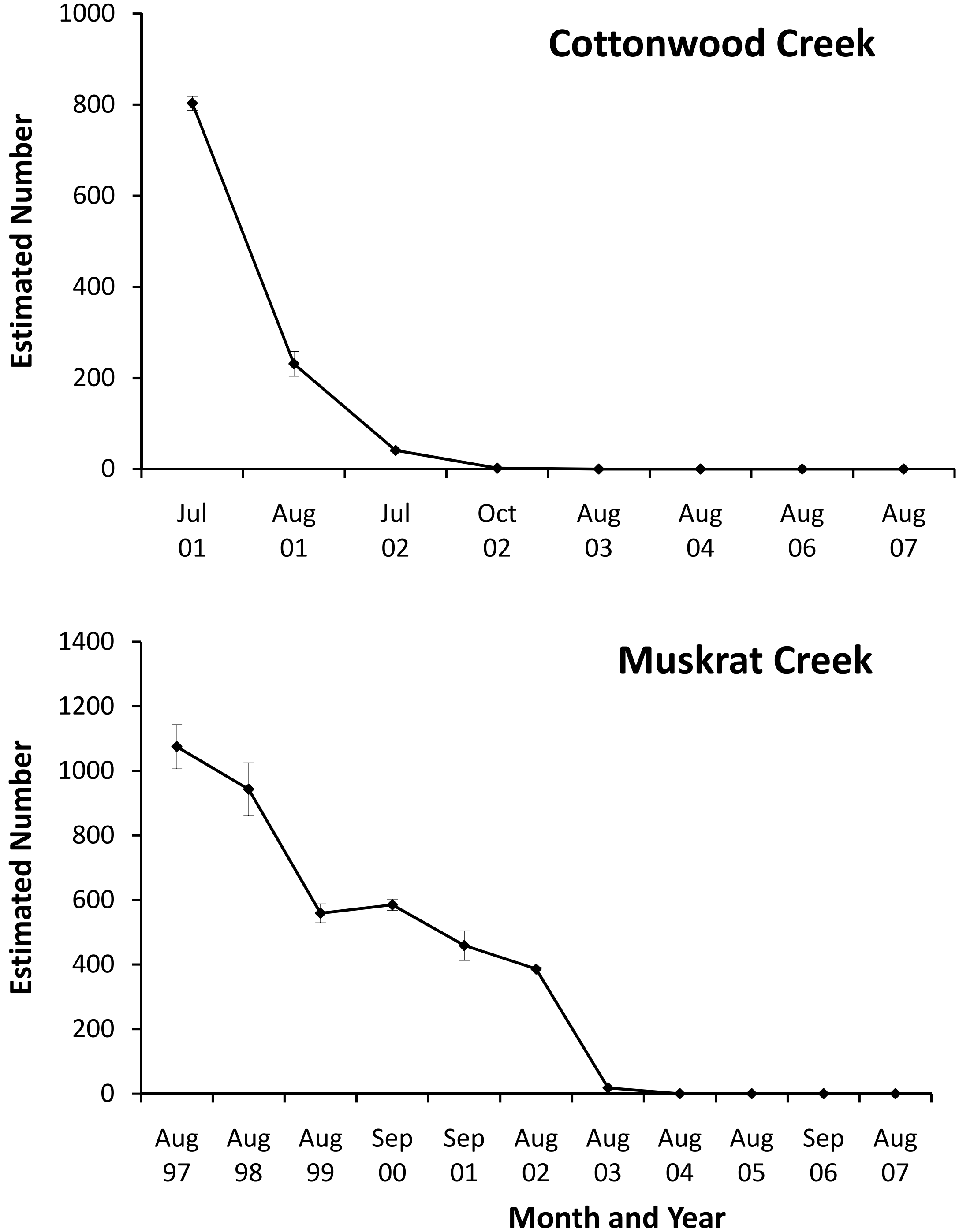

Figure 3.4. Estimated abundances (± 95% CIs) of brook trout 75 mm and longer in Cottonwood and Muskrat creek treatment sections by month and year.

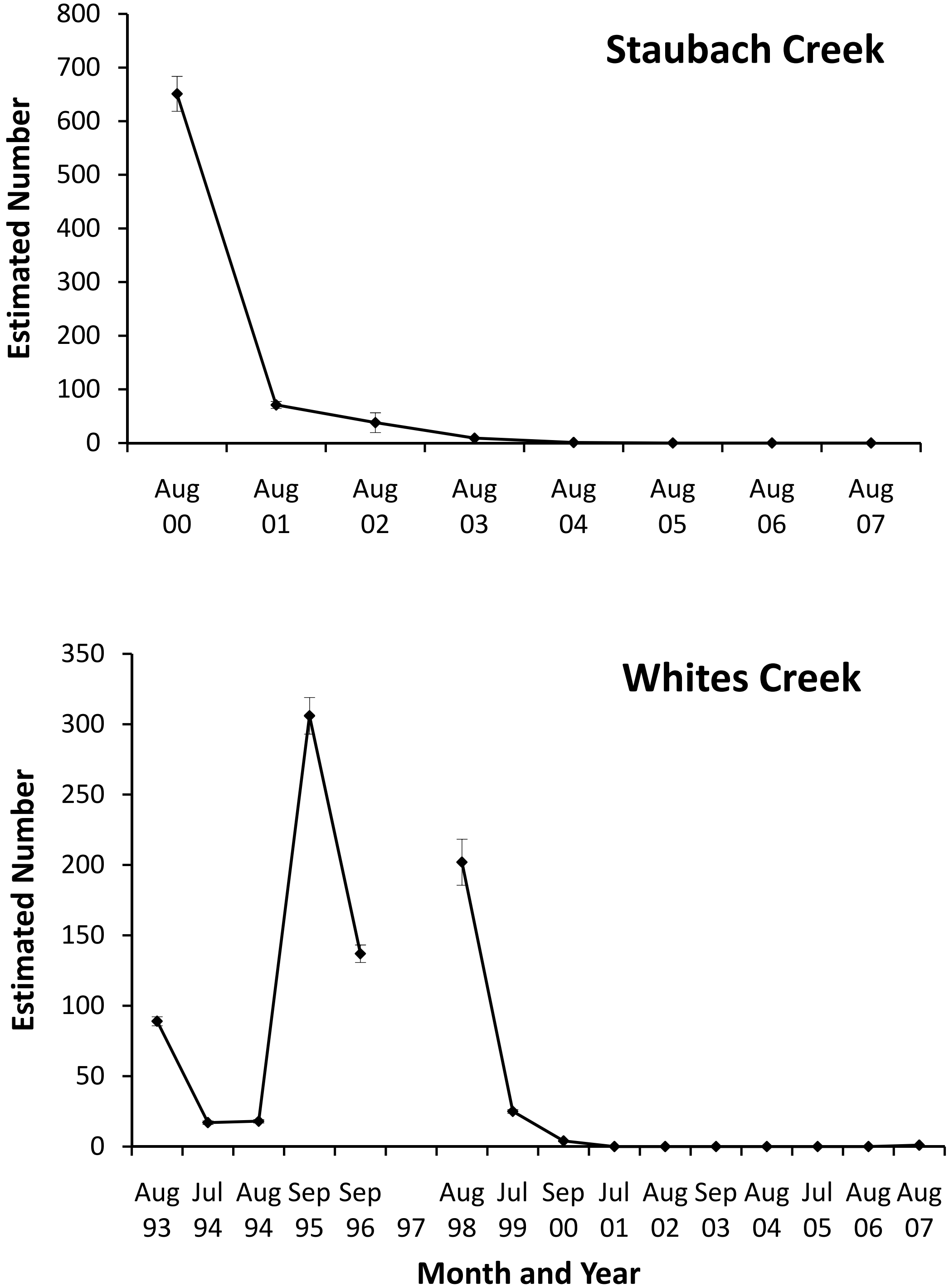

Figure 3.5. Estimated abundances (± 95% CIs) of brook trout 75 mm and longer in Staubach and Whites creek treatment sections by month and year. No estimate was done in Whites Creek during 1997.

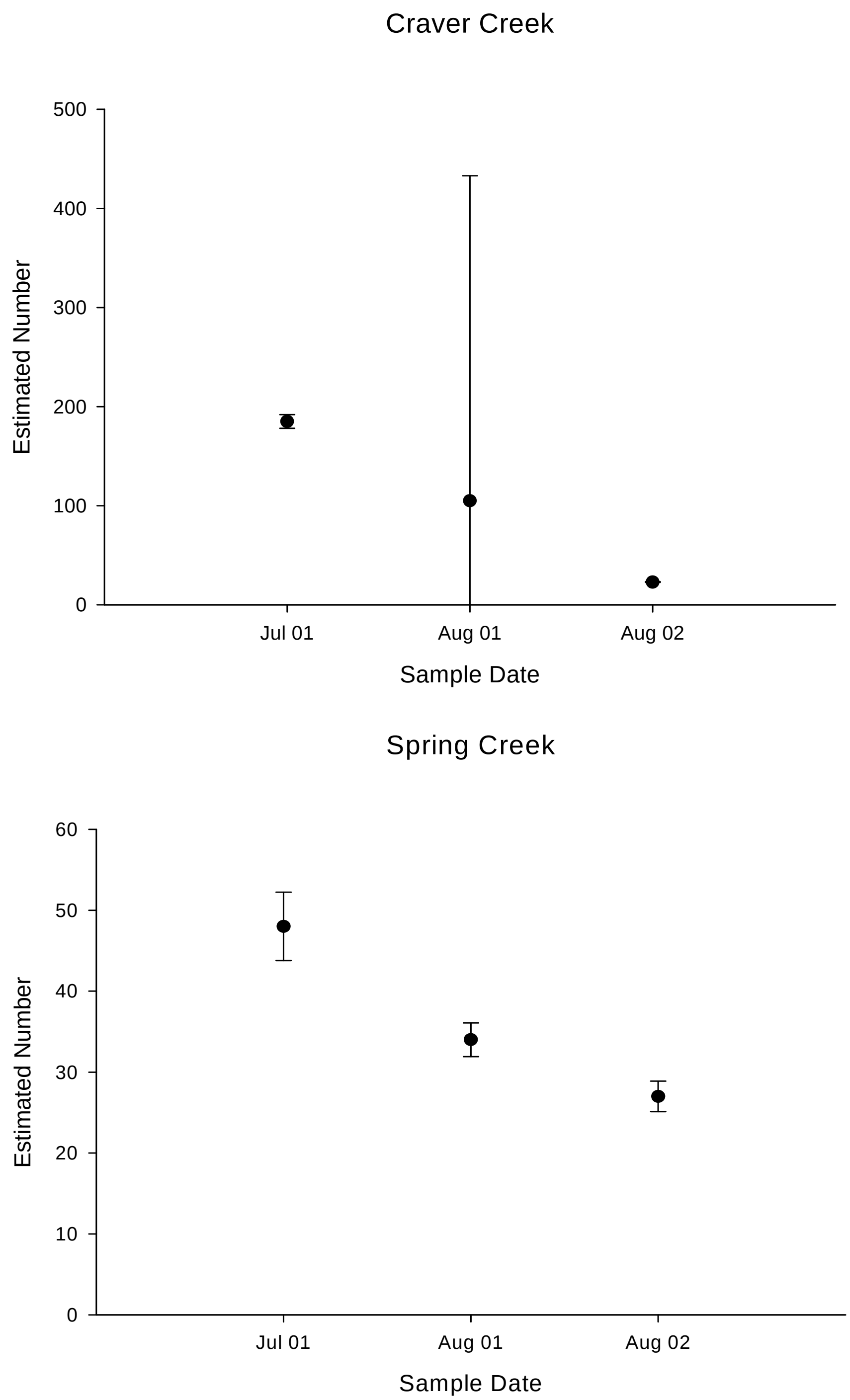

Figure 3.6. Estimated abundance (± SE) of brook trout 75 mm and longer in monitoring sections of Craver Creek (top) and Spring Creek (bottom) from July 2001 to August 2002 by month and year. The wide SE for August 2001 in Craver Creek resulted from a single poor estimate.

CHAPTER 4

EVIDENCE FOR NICHE SIMILARITIES BETWEEN WESTSLOPE CUTTHROAT TROUT AND BROOK TROUT: RECOVERY OF WESTSLOPE CUTTHROAT TROUT POPULATIONS FOLLOWING REMOVAL OF BROOK TROUT

Abstract

I investigated whether 75 mm and longer westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and brook trout (*Salvelinus fontinalis*) occupied similar niches by comparing biomasses, population densities, and condition factors prior to and following total removal of brook trout in 2.4 to 3.0-km reaches of three headwater streams in Montana. I estimated population abundances, biomasses, and their associated 95% confidence intervals for each species using removal estimators. Total trout biomasses significantly increased in all three streams after brook trout were eradicated, indicating that these two species probably have similar niches in these streams and that interference competition may be occurring. Spearman rank correlation tests indicated densities of juvenile and adult westslope cutthroat trout were significantly ($P < 0.05$) and negatively correlated with densities of juvenile and adult brook trout, whereas densities of juvenile and adult westslope cutthroat trout were significantly and positively correlated with each other. Densities of juvenile westslope cutthroat trout were also significantly and negatively correlated with densities of juvenile and adult brook trout during the previous year whereas densities of adult westslope cutthroat trout were not. Densities of westslope cutthroat trout and brook trout had an effect on body condition of individual westslope cutthroat trout, but these effects appeared similar between the two species indicating

interspecific competition was similar to intraspecific competition. I found evidence for size-asymmetric competition in one stream, but not in another. The finding that interspecific competition between brook trout and westslope cutthroat trout was similar to intraspecific competition within westslope cutthroat trout and that interference competition probably occurs between these two species provides insight into mechanisms by which brook trout might displace westslope cutthroat trout.

Introduction

Invasion by exotic species has led to striking changes in native biological communities and has been implicated as a major cause of extinctions (e.g., Miller et al. 1989; D'Antonio and Vitousek 1992) especially in freshwater ecosystems (Arthington 1991; Reinthal and Stiassny 1991; Townsend 1996; Claudi and Leach 1999; Fuller et al. 1999; Kolar and Lodge 2001; Spens et al. 2007). Invasive species affect native species primarily through competitive and predatory interactions among species (Elton 1958). Whereas negative effects of nonnative species on native species are well documented, ecological outcomes of invasions can vary widely (Elton 1958; Burger et al. 2001; Dunham et al. 2002). Invasions of exotic fish species have been caused by intentional releases of exotic sport fish by fishery managers to increase recreational opportunities, unintentional releases by anglers or fishery managers, illegal or unauthorized releases, and natural dispersal of exotic fish after their release (Cambray 2003).

Westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) occur in the Northern Rocky Mountains of the United States and Canada. They historically occupied the broadest range of any cutthroat trout subspecies (Behnke 1992; Shepard et al. 2005); however, their abundance and distribution have declined throughout their range (Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995; Shepard et al. 1997, 2005). Factors associated with this decline include introductions of nonnative fishes, habitat changes, and overexploitation (Hanzel 1959; Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995).

Nonnative brook trout (*Salvelinus fontinalis*) have successfully invaded and now occupy many of the headwater habitats previously occupied by cutthroat trout, often leading to declines or extinction of cutthroat trout populations (MacPhee 1966; Griffith 1970, 1972; Behnke 1992; Gresswell 1988; Krueger and May 1991; McIntyre and Rieman 1995; Shepard et al. 1997; Dunham et al. 2002). Griffith (1988) reviewed the available literature and could not determine whether observed declines and extinctions of cutthroat trout populations following invasion by nonnative salmonids were caused by competitive exclusion (displacement) or replacement following changes in habitat quality. Westslope cutthroat trout populations have been extirpated or severely depressed by other nonnative trout species, primarily rainbow trout (*O. gairdneri*) and brown trout (*Salmo trutta*), in many of the larger streams and rivers within their historical range (e.g., Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995; Shepard et al. 2005). Genetic introgression with rainbow trout and Yellowstone cutthroat trout has led to the genomic extinction of westslope cutthroat trout in many of their historical habitats (e.g., Allendorf and Leary 1988; Gresswell 1988; Allendorf et al. 2001). Westslope cutthroat trout currently persist mainly in isolated headwater refuges over much of their historical range, especially in the Missouri River basin (Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995; Shepard et al. 1997, 2005).

The three most commonly cited mechanisms for displacement of cutthroat by brook trout are competition, predation, and parasite or disease transmission (Dunham et al. 2002). Predation by brook trout on greenback cutthroat trout (*O. c. stomias*) was too low to account for displacement of cutthroat trout by brook trout based on analyses of stomach contents and stable isotopes (McGrath and Lewis 2007). Competition appears to be a more likely mechanism and many researchers have suggested that this competition probably occurs at young ages (Novinger 2000; Shepard et al. 2002; Peterson et al. 2004; Hilderbrand 2003; McGrath and Lewis 2007), but few studies have explicitly tested this (e.g., Novinger 2000; Peterson et al. 2004).

Crowder (1990) suggested that the most rigorous evidence to demonstrate competitive interactions could be gained by showing "repeated changes in growth or abundance when resource levels or competitors are manipulated experimentally." Peterson and Fausch (2003) presented a conceptual framework for a manipulative field experiment to test for population-level mechanisms that promote invasion success and lead to ecological effects. They suggested isolating segments of streams with different physical characteristics and physically removing the invasive species to document the response of the native species. They concluded that this type of experiment would improve the ability to predict ecological effects of invaders and provide information needed to better manage stream salmonid invasions.

Peterson et al. (2004) applied the above technique in relatively short segments (0.8 and 1.2 km) of two streams where they removed brook trout and assessed the response of cutthroat trout over three years. Survival of age-0 and age-1 cutthroat trout increased 13-fold at a mid-elevation site where brook trout were removed versus a control site where brook trout were not removed, but did not find any response at a high-elevation site. They concluded that cold water temperatures limited cutthroat trout recruitment at the high elevation site. Brook trout displaced cutthroat trout by continually invading the high-elevation site and by reducing survival of young cutthroat trout at the mid-elevation site. They were unable to eradicate brook trout from their removal sites because brook trout continued to reinvade: they therefore could not evaluate long-term recovery of cutthroat trout populations.

Montana Fish, Wildlife, and Parks led several collaborative efforts to eradicate brook trout from portions of several streams from 1993 through 2003 (Chapter 3). Total barriers to upstream fish movement were constructed at the lower boundaries of treatment reaches. Eradication efforts were successful in the treatment reaches of four streams and required three to seven years of at least annual removal efforts. Monitoring of four or five sample sections within each of the 2.3 to 3.0-km long eradication reaches in three of these streams occurred throughout brook trout eradication efforts and for at least three years following eradication to assess the response of westslope cutthroat trout following brook trout eradication. To evaluate whether these species occupied similar niches, I compared estimates and 95% confidence intervals (CIs) of biomass (g/m^2) of each species (individuals $\geq$ 75 mm TL) in sympatry prior to brook trout eradication, and of westslope cutthroat trout in allopatry following brook trout eradication. I also examined how densities of juvenile and adult brook trout and westslope cutthroat trout influenced densities and condition factors of juvenile and adult westslope cutthroat trout.

Study Area

Brook trout were eradicated from 2.3 to 3.0-km reaches of Cottonwood, Muskrat, and Whites creeks in the upper Missouri River basin in Montana (Chapter 3; Figure 4.1). These streams were relatively small, cold, neutral to alkaline, and had moderate to low productivity (as indicated by water conductivity measurements; Table 4.1). Westslope cutthroat trout and brook trout were the only fishes present in all these headwater study reaches prior to eradication treatments. Brook trout invasion into Cottonwood Creek appeared to be incomplete because they were present in moderate densities at the lower end of the treatment reach, rare in the middle, and absent from the uppermost portion. Conversely, brook trout were well established throughout treatment reaches in Muskrat and Whites creeks.

Barriers to upstream fish movement were constructed at the lower boundary of each treatment reach. Two were wooden crib barriers and one was made of concrete faced with rock. Barriers had 1.5 to 3.0-m vertical drops with impervious splash pads immediately below them to prevent formation of plunge pools. Tests using marked fish placed below the barriers confirmed that these barriers prevented upstream invasion by nonnative fish (Chapter 3). I monitored four or five sample sections within each brook trout eradication reach during and following brook trout eradication (Figure 4.1).

Climatic conditions during the study were assessed using long-term ($\geq$ 30 years of data) river discharge and climate monitoring sites located near each study stream. I computed deviations of mean annual river discharges and mean annual air temperatures from long-term averages at these climate and discharge monitoring stations. Stream and river discharges in the upper Missouri basin were near average in the early 1990s, above average in the late 1990s, much below average in the early 2000s, and slightly below average in the mid-2000s (Figure 4.2). Average annual air temperatures generally followed an inverse pattern to discharges (Figure 4.2).

Methods

Electrofishing was used to both remove brook trout and estimate abundances of brook trout and westslope cutthroat trout using removal estimators (Van Deventer and Platts 1989). Brook trout were successfully eradicated from treatment reaches in Whites Creek in 2000 and Cottonwood and Muskrat creeks in 2003 (Chapter 3). Long-term abundance estimate sections were established within each treatment reach to track effects of brook trout eradication on biomass and densities of each species (Figure 4.1). I did not test all aspects of species-asymmetric competition because I did not test effects of westslope cutthroat trout on brook trout by removing westslope cutthroat trout (reciprocal removals) from any systems. I estimated population abundances and biomasses for each species (all individuals 75 mm and longer; TL) prior to, during, and following removal of brook trout. Fish were captured using Smith-Root® BP-15, BP-12, and SR-24 model backpack shockers operated at voltages in the range of 100 to 600 V, frequencies under

50 Hz, and pulse widths less than 2 µsec to maximize the number of fish captured while minimizing injury to them (Dwyer et al. 2001).

Electrofishing crews consisted of either two or three people. One member wore the backpack shocker and carried a wand anode while dragging a cable cathode. A second crew member was the primary dip netter and followed the shocker. When available, a third person held a dip net in the stream channel below the two other crewmembers and carried a mesh bucket for transporting captured fish. All electrofishing passes were generally conducted within four hours, except in some sections in Muskrat Creek during 2002 and 2003 where subsequent passes were done the following day. Block nets or fencing material (6.5 mm mesh) were installed between sample sections during most sampling and removal events. The assumption of population closure was met by 1) using either block fences or nets at the upper and lower ends of all sample sections or, in a few cases, locating sections so that they had shallow riffles or velocity barriers at their upper and lower boundaries; 2) using a second netter during most sampling to prevent fish from moving downstream; and 3) the relatively short time it took to complete all sample passes (White et al. 1982). Treatment reaches were broken into 100 to 200-m sections and a subset of these sections, systematically distributed in each treatment reach, were used to monitor population abundances and biomasses (Figure 4.1).

Lengths (total length in mm), species, and pass number were recorded for all captured fish. Weights (g) were measured for almost all captured fish using battery-powered electronic scales (O'Haus® models CS and CL); however, during a few sampling events weights were not recorded because of equipment malfunctions. All fish were weighed to the nearest gram, even though scale accuracy was 0.1 g.

Density Estimates

Numbers of fish 75 mm and longer were estimated using removal estimators (Van Deventer and Platts 1989). Removal estimators consistently underestimate true abundances, especially when only two passes are made and capture probabilities are less than 0.90 (Riley and Fausch 1992). White et al. (1982) recommended three or more passes unless the capture probability is 0.8 or higher. Riley and Fausch (1992) suggested that three passes reduced estimate bias and showed through simulation that bias was low at capture probabilities above 0.9 and relatively low at capture probabilities over 0.8. I found that when the ratio of the number of captured fish to the number estimated was 0.7 or higher, deviations of estimates from true populations were clustered near zero (Chapter 2). Of the 107 removal estimates I made, 82 were two-pass estimates, 24 were three-pass estimates, and one was a four-pass estimate. I never captured less than 40% of the estimated population (mean=95%, range: 40 to 100%). About 75% of all two-pass estimates had estimated capture probabilities of 0.8 or higher.

When no fish were captured on the second pass of a two-pass estimate, total abundance was assumed to be the total number of fish captured on the first pass. Four instances occurred in which abundances could not be estimated using the standard estimator because of non-declining captures, two for brook trout in Whites Creek (either one or two fish captured during each pass) and two for westslope cutthroat trout in

Muskrat Creek (three fish captured during each pass in one case and one fish captured in the first pass followed by three fish in the second pass). In these cases, I use the total number of captured fish as the estimated number. Rhis protocol probably led to an underestimation bias because of my assumption of a capture probability of one, even though it was probably less than one, but I had no way to test this assumption.

Abundance estimates for juvenile (75 to 149 mm) and adult ($\geq$ 150 mm) westslope cutthroat trout and brook trout in each sample section were made and summed to compute densities (number/ha) by year. I derived the estimated abundance in each size class by multiplying the proportion captured within each size class by the total estimated abundance of fish 75 mm and longer. Estimated densities were computed by summing estimated abundances and areas sampled across sample sections within each treatment reach by year and dividing total abundance by total area sampled.

Distributions of estimated densities of juveniles and adults by species were plotted to check for normality. I could not reliably test these distributions statistically because of relatively low sample sizes (< 32). Visual inspection of frequency histograms and qq-normal plots indicated that distributions of juvenile and adult densities were highly skewed with many zeros, especially for brook trout following their removal. Consequently, I transform density estimates using natural log transformations as $\log_n$(density + 1). I added one to density estimates to avoid the problem of $\log_n(0)$ being an undefined number and because $\log_n(1)$ equals zero. Because standardization of density estimates to the number of fish per hectare resulted in relatively high numbers whenever fish were present, I assumed that any positive bias introduced by adding one to these density estimates was minor.

I used negative binomial regression to evaluate how estimated abundances of juvenile or adult westslope cutthroat trout (tested as the response variable) might be influenced by densities of juvenile and adult brook trout (covariates). Density of the life-stage of westslope cutthroat trout not tested as the response variable was also included as a covariate. The area of stream sampled (m^2) was included in these regressions as an offset (included in the intercept term). Data were available for 30 sampling events. I evaluated all potential models, including those with interaction terms, and used the corrected Akaike Information Criteria (AICc; Akaike 1974; McQuarrie and Tsai 1998) with both the intercept and dispersion parameter estimates included as estimated variables to determine the most plausible models. This negative binomial regression analysis was done using the “glm.nb” function within the “MASS” package in the “R” statistical program (Ripley 2010).

Biomass Estimates

Estimates of total weight (g) were made for fish 75 mm and longer by species for each long-term sample section (solid triangles on Figure 4.1) by year using a new model-based finite population correction factor method that I developed (FPCM in Chapter 2). For those few estimate events cited above where non-declining captures prevented me from making removal estimates, total weights of captured fish were assumed to be the total weight estimate. These few total weight estimates were probably under-estimates, though the degree of bias is unknown. Sample mean weights and variances for use in the FPCM and $FPCM_{reg}$ biomass estimators were estimated, by species, from all fish sampled within the treatment reach of each stream during each sample period. This was necessary because captured fish were only counted and not weighed and measured because of time constraints in some sample sections during a few of the sampling events. This occurred relatively infrequently and those sections where fish were only counted were located throughout the treatment reach, so no systematic bias should be associated with this sampling. Because fish that were captured and weighed during any given sampling event were captured throughout a treatment reach, I assumed that mean weights and variances in weight for these sampled fish represented each sample section.

Estimated weights, variances, and sampled area were summed across sample sections within treatment reaches by year. Total weights were divided by total sample area to derive total biomass estimates (g/m^2) by treatment reach and year. After summing total variances and dividing by sample area to estimate variance per area, standard errors were computed as the square-root of these variances to estimate 95% CIs. For this analysis CIs were computed using the normal distribution rather than the lognormal distribution used in Chapter 2, which resulted in slightly wider confidence intervals. I assumed that valid comparisons could be made for estimates of population densities and biomasses among years within each stream because I sampled relatively large proportions of the total treatment reach within each stream during each year, sampled nearly identical sections of each treatment reach each year, and converted these estimates to number or weight per area.

Condition Factors

Because slopes of $\log_{10}$(length) to $\log_{10}$(weight) regressions were near 3.0 for westslope cutthroat trout during all years (Table 4.2), an assumption of isometric growth was reasonable. I therefore computed Fulton-type condition factors as these are easier to compare among years than regression metrics (Pope and Kruse 2007). I computed the condition factor for each individual westslope cutthroat trout captured within treatment reaches for which both length and weight had been recorded:

$$K = \frac{100{,}000 * W}{L^3}, \qquad \text{[Equation 1]}$$

where K is condition, W is weight (g), and L is length (TL, mm; Anderson and Gutreuter 1983). I only included westslope cutthroat trout that were captured from July through October to reduce the influence of the weight of sex products in mature adults. Visual inspection of frequency histograms and qq-normal plots indicated condition factors were nearly normally distributed. I conducted two separate analyses using fish condition. First, I tested for correlations (Spearman rank correlations) among mean condition factors of juvenile (75 to 149 mm) and adult ($\geq$ 150 mm) westslope cutthroat trout, estimated densities of juvenile and adult westslope cutthroat trout, estimated densities of juvenile and adult brook trout, annual deviations in discharges, and annual deviations in air temperatures by sample occasion across all streams and years.

Second, I assessed relative effects of both intra- and interspecific competition and size-asymmetric competition for food resources in the two streams that brook trout had successfully invaded (Muskrat and Whites creeks) by determining effects that density of each species (by 10-mm size group) had upon body condition of each individual cutthroat trout. I assumed that condition factors of individual cutthroat trout integrated their use of both food and space resources during the summer in these headwater streams (Chapman 1966; Chapman and Bjornn 1969). The body condition factor metric represents a relatively short-term response (month to months) of an individual to its environment (e.g., Kebus et al. 1992).

Roughgarden's (1979) asymmetric competition function was used to estimate and test the magnitude of size-dependent competition and the potential for competitive asymmetry using nonlinear regression. The competitive effect of individual *j* on individual *i* is modeled as:

$$\alpha_{i,j}(x_i, x_j; \sigma_v^2, \kappa) = \exp\left(\sigma_v^2 \kappa^2\right) \exp\left[\frac{-\frac{1}{2}\left(x_j - x_i + 2\sigma_v^2 \kappa\right)^2}{2\sigma_v^2}\right], \qquad \text{[Equation 2]}$$

where $\boldsymbol{x_i}$ and $\boldsymbol{x_j}$ are the $\log_n$(lengths) of the competing fish, σ_v^2 is breadth of the competition parameter, and $\boldsymbol{\kappa}$ is the size-asymmetry parameter. The competition function is a Gaussian curve that has been normalized to express the total competition (area under the curve) of individual *j* on individual *i* based on the size difference between the two individuals. Breadth of competition (σ_v^2) indicates how dissimilar in size an individual can be and still compete strongly with the focal individual. Note that a larger fish will have a more substantial effect on a smaller fish than vice versa if the size-asymmetric variable ($\boldsymbol{\kappa}$) is positive. To calculate the competitive effect of the population (all *j*) on a focal individual (individual *i*), this competition function is summed over the estimated densities of all fish 75 mm and longer by size. The size groups were 75 to 79 mm and 80 to 299 mm by 10-mm increments, for a total of 23 size groups. I partitioned total abundance estimates of fish 75 mm and longer into these 23 length groups based on the proportion of fish captured within each length group. I used the non-linear regression model with mixed-effects package "nlme" (Pinhero et al. 2008) in the "R" statistical package (R Development Core Team 2009; http://cran.r-project.org) to test for relative effects of competition by brook trout on westslope cutthroat trout and the presence of size-asymmetric competition on body condition (*K* of Equation 1, expressed as k_i in Equation 3, below) of individual westslope cutthroat trout in a regression equation:

$$k_i = Year + a\sum_{j}^{all\,WCT}\alpha_{i,j}(x_i, x_j; \sigma^2_{WCT}, \kappa) + b\sum_{j}^{all\,BT}\alpha_{i,j}(x_i, x_j; \sigma^2_{BT}, \kappa), \qquad \text{[Equation 3]}$$

where each $\boldsymbol{\alpha}_{ij}$ is computed using Equation 2 with the letter subscripts identifying westslope cutthroat trout (WCT) and brook trout (BT). Summing the effects of all fish in the population on the condition factors of all westslope cutthroat trout in the population provides an index of the relative competitive effects of each species on use of food and space by westslope cutthroat trout 75 mm and longer during the July through October period.

I tested models that allowed for the same or different coefficients for brook trout and westslope cutthroat trout competition effects ("***a***" and "***b***"), similar or different individual breadths of competition for brook trout and westslope cutthroat trout ($\boldsymbol{\sigma}^2_{BT}$ and

σ^2_{WCT}), and whether competitive size-asymmetry (κ) was present or not. Values for all of these variables (a, b, σ^2_{BT} , σ^2_{WCT}, and , κ) were estimated simultaneously by non-linear modeling that applied the competition function for each species in the non-linear regression equation. I was unable to evaluate size-asymmetry by species because nonlinear models would not converge because of too many variables being estimated, so I assumed that if size-asymmetry was included in a model it was equal between the two species. Year was treated as a random effect in all models. Model selection was done using the Bayesian Information Criteria (BIC; Schwarz 1978; Pinhero et al. 200). The assumption inherent in this analysis is that westslope cutthroat trout with higher condition factors (k_i) are better competitors for food and space resources than those with lower condition factors.

When testing effects of fish species, fish density and size-asymmetry on the variation in condition factors of individual westslope cutthroat trout using the Roughgarden (1979) competition function, all the data were initially combined and stream and all competition variables were entered into the model as fixed effects and year was entered as a random effect. Stream effect was significant, so I conducted separate analyses for each stream. Because I determined that brook trout had not fully affected westslope cutthroat trout populations in the treatment reach of Cottonwood Creek because brook trout had not fully invaded this stream, I removed it from the analysis and used only Muskrat and Whites creeks. The effect of year was considered marginal for all models in both streams (S.D. of year was about half of the S.D. of the residual; Tables 4.6 and 4.7).

Statistical Testing

All statistical tests use a significance level of $P < 0.05$, unless otherwise indicated. I use SYSTAT© (version 11, SYSTAT 2004; http://www.systat.com) to conduct initial data explorations and the "R" statistical program to conduct final analyses (R Development Core Team 2009; http://cran.r-project.org). Overlap of 95% CIs was used to determine if significant differences existed between total biomass of brook trout and westslope cutthroat trout in sympatry before brook trout eradication and biomass of westslope cutthroat trout in allopatry after brook trout eradication. I used 95% CIs because these are a conservative measure for detecting significant differences. I plotted estimated biomasses in stacked bar graphs to evaluate the relative contribution of each species and illustrate the timing in the response of westslope cutthroat trout following the removal of brook trout.

I tested for associations between estimated densities and conditions of juvenile and adult westslope cutthroat trout and juvenile and adult brook trout using Spearman rank correlation tests because the assumption of normality for estimated densities could not be met. I corrected for the effect of tied ranks in this data set (up to seven estimates of zero brook trout) by adjusting the estimated level of significance (Daniel 1978). Negative binomial regression analysis in the "R" statistical package uses a log-link function; therefore natural logs of estimated numbers of juvenile and adult westslope cutthroat trout were the dependent variables in the models. I considered as plausible those models for which the AIC values were the lowest or were within 3 units of the lowest AIC model. After determining the most plausible models, I further evaluated these models using the "glm" procedure in "R" to evaluate the distribution of residuals and the assumption of normality of errors and to determine if a few data points exerted too much influence on the regression model (leverage; Crawley 2007).

Results

Biomass

Eradication of brook trout from the treatment reaches was accomplished in two to seven years (Figures 4.3 through 4.6). Populations of westslope cutthroat trout rebounded two to four years after the successful eradication of brook trout (Figures 4.3 through 4.6; Appendix D). Biomass estimates (g/m^2) of westslope cutthroat trout in allopatry three to four years following brook trout eradication were significantly higher than estimates of total biomass for both species in sympatry at the start of removals in all three streams (Figures 4.3 and 4.4). Some longitudinal differences appeared to be present in westslope cutthroat trout biomasses over time during and following the removal of brook trout, with westslope cutthroat trout shifting upstream in Cottonwood and Whites creeks and downstream in Muskrat Creek (Appendix D).

Densities

Densities of juvenile westslope cutthroat trout did not increase appreciably in any of the streams until brook trout had been eradicated. Densities of brook trout in

Cottonwood Creek were slightly lower than densities of westslope cutthroat trout at the start of removal efforts (Figure 4.5). Brook trout were eradicated from Cottonwood Creek within two years and densities of westslope cutthroat trout responded by increasing to levels higher than those of both westslope cutthroat trout and brook trout at the start of brook trout eradication efforts.

Densities of brook trout at the start of removal efforts were higher in Muskrat Creek than in the other two streams (Figure 4.6, top). After removal efforts began, juvenile brook trout densities did not decline significantly until 2000 after removal efforts had eliminated most of the adult brook trout and could be focused more on juveniles.

Whites Creek had relatively low densities of juvenile brook trout, but high densities of adult brook trout, when removal efforts began (Figure 4.6; bottom). The relatively high densities of adults resulted in a relatively high estimate of total brook trout biomass (Figure 4.3; bottom graph, year 1993). Densities of juvenile westslope cutthroat trout rose slightly in 1995; two years after brook trout removal efforts began. They subsequently declined in 1997 following a rebound of both juvenile and adult brook trout in 1996. Juvenile westslope cutthroat trout densities increased from 1998 through 2000 as brook trout were successfully eradicated. Densities of adult westslope cutthroat trout lagged about one year behind densities of juvenile westslope cutthroat trout through 2000. The westslope cutthroat trout population fell to low levels between 2000 and 2005, probably in response to prolonged drought (Figure 4.2) and improper livestock grazing, but rebounded strongly through 2006 and 2007.

Densities of both juvenile and adult westslope cutthroat trout were negatively and significantly correlated with densities of both juvenile and adult brook trout and annual discharge deviations from the historical mean (Table 4.3). Densities of juvenile westslope cutthroat trout were positively and significantly correlated with densities of adult westslope cutthroat trout and negatively and significantly correlated to densities of juvenile and adult brook trout both in the current and previous year. Densities of adult westslope cutthroat trout were also negatively and significantly correlated to annual air-temperature deviations from the historical mean temperature.

Estimates of regression coefficients in negative binomial models were generally similar among different models, indicating stability among models (Tables 4.4 and 4.5). Several negative binomial regression models were similarly plausible for explaining the variation in abundance of juvenile westslope cutthroat trout. Density of adult westslope cutthroat trout was included and significant in all plausible models and was positively associated with estimated numbers of juvenile westslope cutthroat trout (Table 4.4). Densities of juvenile and adult brook trout were each included in two plausible models, but their coefficients were only significant for one model each. Densities of juvenile and adult brook trout were negatively associated with estimated abundances of juvenile westslope cutthroat trout in all models in which they were included. When both densities of juvenile and adult brook trout were included together, neither was significant nor were the coefficients for any of the interaction terms significant in models that included interactions.

The most plausible negative binomial regression model that explained the variation in abundances of adult westslope cutthroat trout included densities of juvenile westslope cutthroat trout, juvenile brook trout, and adult brook trout (Table 4.5). Densities of juvenile westslope cutthroat trout and adult brook trout were positively associated with estimated abundances of adult westslope cutthroat trout. Density of juvenile brook trout was negatively associated with estimated abundances of adult westslope cutthroat trout. Models that included interaction terms had AIC values near the best model, but none of the interactions were significant.

Condition Factors

Little correlation existed between mean condition factors of juvenile or adult westslope cutthroat trout and most variables tested (densities by species and life-stage and discharge and temperature deviations). Significant correlations were observed between condition factors of juvenile westslope cutthroat trout and condition factors of adult westslope cutthroat trout (positive), condition factors of adult westslope cutthroat trout and density of juvenile westslope cutthroat trout (negative), and condition factors of adult westslope cutthroat trout and deviation of annual discharge from the historical mean discharge (positive, Table 4.5).

For Whites Creek the simplest model was statistically as good or better than more complex models (Table 4.6). This simple model treated competition by brook trout and westslope cutthroat trout the same (i.e., equal coefficients for both westslope cutthroat trout, "***a***", and brook trout, "***b***", and an equal breadth of competition [σ^2] for individuals of each species) and excluded the size-asymmetry parameter, For Muskrat Creek the model that treated competition by brook trout and westslope cutthroat trout the same but included a size-asymmetry parameter was better than any other model; however, the size-asymmetry coefficient was not significant ($P > 0.15$; Table 4.7).

These results indicated that brook trout and westslope cutthroat trout densities similarly affected westslope cutthroat trout body conditions during the summer growth period over a range of densities and body sizes typically found in headwater stream environments. I found some evidence of differential size-based competition in Muskrat Creek, but not in Whites Creek. The breadth of the competition parameter, σ^2, for individuals was included in models for both Whites and Muskrat creeks, but was not significantly different between the two species, indicating that similar-sized fish competed with each other, regardless of species.

Discussion

Westslope cutthroat trout populations in these treatment reaches rebounded in spite of repeated annual electrofishing, effects from improper livestock grazing in Whites Creek, and persistent drought conditions in the region from 2000 to 2007 (Figure 4.2). Additionally, a total of 226 age-1 and older westslope cutthroat trout from the treatment reach in Muskrat Creek were moved upstream to the headwater portion of this stream above an impassable waterfall in 1997, 1998, and 2001 to expand and better protect this population. I suspect that westslope cutthroat trout in the treatment reach of Muskrat Creek would have rebounded faster had I not removed these fish. The westslope cutthroat trout populations in Muskrat and Whites creeks rebounded sufficiently such that Montana Fish, Wildlife, and Parks harvested gametes from them to re-establish or start westslope cutthroat trout populations in other streams as part of their conservation efforts.

A few adult brook trout were found in the lower portions of the Muskrat and Whites creek treatment reaches during 2007 after brook trout had been successfully eradicated from these treatment reaches. I suspected that these brook trout were moved above the lower boundary fish barriers by members of the public. These brook trout were again eradicated from treatment reaches in both streams by 2008 with moderate removal efforts. Movement of nonnative fish above barriers purposely constructed to exclude them by the public has been recognized as a significant challenge to conservation efforts (e.g., Harig et al. 2000).

Inference of Competition between Brook and Cutthroat Trout

Brook trout and westslope cutthroat trout 75 mm and longer apparently occupied similar niches in these streams as judged by the recovery of westslope cutthroat trout biomasses to higher levels than those of both species combined in sympatry. Concordant results from correlation analyses and application of Roughgarden's (1979) competition function also suggested that brook trout affected cutthroat trout. These results could have been even more compelling had I collected several years of information prior to initiation of removal efforts to account for potential year effects.

The competition modeling results suggest that for these two species similar-sized individuals, irrespective of their species, were probably using similar habitats or foods or both. I only tested these effects for fish 75 mm and longer and competitive effects may be more even pronounced between age-0 brook trout and cutthroat trout (Novinger 2000; Shepard et al. 2002; Peterson et al. 2004; Hilderbrand 2003; McGrath and Lewis 2007; but see Koenig 2006). Unfortunately, I could not estimate abundance or condition of age-0 westslope cutthroat trout during this study because of their extremely small size (often < 50 mm at the end of their first summer) and concerns about mortality of these fry during sampling.

Interference competition (Birch 1957; Case and Gilpin 1974; Hughes and Grand 2000) may be occurring between westslope cutthroat trout and brook trout, suggested by the significant increases in total biomasses I documented after eradication of brook trout. My competition function analysis of body condition suggests that exploitive competition between these two species is also likely occurring during the summer growth period.

Thomas (1996) observed that young brook trout inhibited the foraging efficiency of juvenile Colorado River cutthroat trout. *O. c. pleutiticus*, in a controlled laboratory setting. She suggested that this inhibition might be the mechanism responsible for decreased growth rates of cutthroat trout she documented in the wild. Cummings (1987) observed that juvenile brook trout excluded juvenile greenback cutthroat trout *O. c. stomias* from more profitable stream positions in Hidden Creek, Colorado. Interference competition between brook trout and westslope cutthroat trout may be a function of the incompatibility between the hierarchical behavior of cutthroat trout that prefer pool habitats (e.g., Kalleberg 1958; Chapman 1966; Chapman and Bjornn 1969; Bachman 1984; Shepard et al. 1984; Nakano and Furukawa-Tanaka 1994; Gowan 2007) and the territorial behavior exhibited by brook trout (e.g., Newman 1956; Griffith 1972; Fausch and White 1981; Hakala and Hartman 2004; Zimmerman and Vondracek 2006; Buys et al. 2009).

Whereas the competitive mechanisms that allow brook trout to displace westslope cutthroat trout are still in question, my results all indicated that interspecific competition between brook trout and westslope cutthroat trout may be as strong, or stronger, than intraspecific competition among westslope cutthroat trout. These results support previous inferences that competition is probably a stronger mechanism for displacement of cutthroat trout by brook trout than predation (McGrath and Lewis 2007) and that it probably occurs at young ages (Novinger 2000; Shepard et al. 2002; Peterson et al. 2004; Hilderbrand 2003; McGrath and Lewis 2007). Competition among age-0 fish may be even stronger than what I observed among older fish; body size-asymmetry probably plays a more important role in competition among age-0 fish than among older fish based on results from other species. Large age-0 coho salmon (*O. kistuch*) and steelhead trout (*O. mykiss*) dominated smaller individuals; large individuals adopted aggressive fighting behaviors whereas smaller individuals were passive (Young 2003). Young (2004) concluded that because coho fry emerged earlier and maintained a size advantage over steelhead fry, interspecific competition was strongly asymmetrical in favor of coho and that habitat selection by both species was strongly dependent upon densities of coho fry. This mechanism may explain the commonly reported dominance of age-0 brook trout over age-0 cutthroat trout (Griffith 1974) and may be a major factor responsible for the displacement of cutthroat trout by brook trout (Novinger 2000; Shepard et al. 2002; Peterson et al. 2004; Hilderbrand 2003; McGrath and Lewis 2007).

Growth of native age-0 brook trout in Ontario, Canada, declined following the emergence of nonnative rainbow trout, *O. mykiss*, fry (Rose 1986). Age-0 rainbow trout impaired the growth of age-0 brook trout, even though age-0 rainbow trout were smaller than age-0 brook trout because they emerged later. Rose (1986) suggested that the reduced growth he observed for age-0 brook trout was related to the much higher densities of age-0 rainbow trout than of age-0 brook trout. He speculated that the reduction in growth of age-0 brook trout he observed could lead to higher overwinter mortality and that this might be a mechanism by which rainbow trout exclude brook trout. In my study, later emergence by cutthroat trout was apparently not off-set by their higher densities immediately after emergence, perhaps because of behavior differences between age-0 rainbow trout and age-0 cutthroat trout. This might be a fruitful area for future research.

Though I did not remove westslope cutthroat trout from any streams to fully test for species-asymmetric competition by doing reciprocal removals, several studies (McGrath and Lewis 2007; McHugh and Budy 2006; McHugh et al. 2008; Shemai et al. 2007) and my observations indicate that species-asymmetric competition between brook trout and cutthroat trout probably occurs with brook trout usually out-competing cutthroat trout. Brook trout can potentially out-compete and displace cutthroat trout wherever abiotic conditions allow brook trout to invade (Fausch 2007). Displacement of westslope cutthroat trout by brook trout is common, especially in the upper Missouri River basin of

Montana (Shepard et al.1997, 2005). Species-asymmetric competition has also been shown to exist among co-occurring native cutthroat trout and Dolly Varden charr, *Salvelinus malma*, in two lakes in British Columbia, Canada (Jonsson et al. 2008).

Evidence for size-asymmetric competition was only found in Muskrat Creek, perhaps because its physical characteristics differ from those of Whites Creek, which is a smaller stream with a long intermittent reach above the area I sampled. It may be that larger trout in Whites Creek do not accrue any additional benefits from their larger size because of the relatively small and isolated habitats there. Rosenfeld and Taylor (2009) indicated that larger trout may need to move downstream out of small headwater areas of streams to meet their energetic demands, which I have observed for larger westslope cutthroat trout. These results support the conclusions of Case (2000) that "the outcome of competition depends upon environmental conditions and sometimes on the initial conditions."

My correlation results suggest that intraspecific competition may be manifested as a density-dependent effect between condition of adult cutthroat trout and densities of juvenile cutthroat trout. This finding lends support to the idea that as trout grow larger it is harder for them to meet their energetic demands (Rosenfeld and Taylor 2009), especially in the face of high densities of conspecifics, and suggests that larger trout may leave these headwater areas in accord with the self-thinning hypothesis for stream-resident salmonids (Bohlin et al. 1994; Dunham and Vinyard 1997).

Abiotic Factors that Influenced Competition

Temperature was negatively correlated with both density and condition of westslope cutthroat trout, whereas discharge was negatively correlated to density, but positively correlated to condition of westslope cutthroat trout (Table 4.3). It appears that abundances of both adult and juvenile westslope cutthroat trout were higher during cooler years, probably in response to more favorable conditions for growth and survival (e.g., Bear et al. 2007). It is possible that high annual discharges result in fewer low-velocity, shallow refuge areas needed by juvenile westslope cutthroat trout, but that adult westslope cutthroat trout can take advantage of increases in channel volume created by higher discharges (e.g., Fausch and Northecote 1992; Rosenfeld and Taylor 2009).

Electrofishing Injury Implications

Westslope cutthroat trout populations in all three streams rebounded relatively rapidly after brook trout populations had been suppressed, despite repeated intensive electrofishing sampling for many consecutive years. Concern exists about electrofishing injury of salmonids (e.g., Gatz et al. 1986; Reynolds et al. 1988; Sharber and Carothers 1988; McMicheal 1993; Hollender and Carline 1994), especially for native species (Nielsen 1998; Dwyer et al. 2001), although some question whether individual effects translate to population effects (Dalbey et al. 1996; Schill and Elle 2000).

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Literature Cited

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716-723.

Allendorf, F. W. and R. F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. Conservation Biology 2:170-184.

Allendorf, F. W., R. F. Leary, P. Spruell, and J. K. Wenburg. 2001. The problems with hybrids: setting conservation guidelines. Trends in Ecology and Evolution 16:613-622.

Anderson, R. O., and S. J. Gutreuter. 1983. Length, weight, and associated structural indices. Pages 283-300 *in* L. A. Nielsen and D. L. Johnson, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Arthington, A. H. 1991. Ecological and genetic impacts of introduced and translocated freshwater fishes in Australia. Canadian Journal of Fisheries and Aquatic Sciences 48(Supplement 1):33-43.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113:1-32.

Bear, E. A., T. E. McMahon, and A. V. Zale. 2007. Comparative thermal requirements of westslope cutthroat trout and rainbow trout: implications for species interactions and development of thermal protection standards. Transactions of the American Fisheries Society 136:1113-1121.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Birch, L. C. 1957. The meanings of competition. American Naturalist 856:5-18.

Bohlin, T., C. Dellefors, U. Faremo, and A. Johlander. 1994. The energetic equivalence hypothesis and the relation between population-density and body-size in stream-living salmonids. American Naturalist 143:478-493.

Burger, J. C., M. A. Patten, T. R. Prentice, and R. A. Redak. 2001. Evidence for spider community resilience to invasion by non-native spiders. Biological Conservation 98:241-249.

Buys, D. J., R. H. Hilderbrand, and J. L. Kershner. 2009. The effects of varied densities on the growth and emigration of adult cutthroat trout and brook trout in fenced stream enclosures. Western North American Naturalist 69:371-381.

Cambray, J. A. 2003. Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. Hydrobiologia 500:217-230.

Case, T. J. 2000. An illustrated guide to theoretical ecology. Oxford University Press, New York.

Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences 71:3073-3077.

Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. American Naturalist 100: 345-357.

Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153-176 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams, Institute of Fisheries, University of British Columbia, Vancouver.

Claudi, R., and J. H. Leach. 2000. Nonindigenous freshwater organisms: vectors, biology and impacts. Lewis Publishers, London.

Crawley, M. J. 2007. The R book. John Wiley and Sons, West Sussex, England.

Crowder, L. B. 1990. Community ecology. Pages 609-632 *in* C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Cummings, T. R. 1987. Brook trout competition with greenback cutthroat trout in Hidden Creek, Colorado. Master's thesis. Colorado State University, Fort Collins.

Daniel, W. W. 1978. Applied nonparametric statistics. Houghton Mifflin Company, Boston.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. Annual Review of Ecology and Systematics 23:63-87.

Dalbey, S. R., T. E. McMahon, and W. Fredenberg. 1996. Effect of electrofishing pulse shape and electrofishing-induced spinal injury on long-term growth and survival of wild rainbow trout. North American Journal of Fisheries Management 16:560-569.

Dunham, J. B., S. B. Adams, R. E. Schroeter, and D. C. Novinger. 2002. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. Reviews in Fish Biology and Fisheries 12:373-391.

Dunham, J. B., and G. L. Vinyard. 1997. Relationship between body mass, population density, and the self-thinning rule in stream-living salmonids. Canadian Journal of Fisheries and Aquatic Sciences 54:1025-1030.

Dwyer, W. P., B. B. Shepard, and R. G. White. 2001. Effect of backpack electroshock on westslope cutthroat trout injury and growth 110 and 250 days posttreatment. North American Journal of Fisheries Management 21:646-650.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Harvard University Press, Cambridge, Massachusetts.

Fausch, K. D. 2007. Introduction, establishment and effects of non-native salmonids: considering the risk of rainbow trout invasion in the United Kingdom. Journal of Fish Biology 71:1-32.

Fausch, K., and T. Northcote. 1992. Large wood debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682-693.

Fausch, K. D., and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220-1227.

Fuller, P. L., L. G. Nico, and J. D. Williams. 1999. Nonindigenous fishes introduced into inland waters of the United States. American Fisheries Society, Special Publication 27, Bethesda, Maryland.

Gatz, A. J., Jr., J. M. Loar, and G. F. Cada . 1986. Effects of repeated electroshocking on instantaneous growth of trout. North American Journal of Fisheries Management 6:176-182.

Gowan, C. 2007. Short-term cues used by foraging trout in a California stream. Environmental Biology of Fishes 78:317-331.

Gresswell, R. E. 1988. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.

Griffith, J. S., Jr. 1970. Interaction of brook trout and cutthroat trout in small streams. Doctoral dissertation. University of Idaho, Moscow.

Griffith, J. S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada 29:265-273.

Griffith, J. S., Jr. 1974. Utilization of invertebrate drift by brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki)* in small streams in Idaho. Transactions of the American Fisheries Society 103:440-447.

Griffith, J. S., Jr. 1988. Review of competition between cutthroat trout and other salmonids. American Fisheries Society Symposium 4:134-140.

Hakala, J. P., and K. J. Hartman. 2004. Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. Hydrobiologia 515: 203-213.

Hanzel, D. A. 1959. The distribution of the cutthroat trout (*Salmo clarki*) in Montana. Proceedings of the Montana Academy of Sciences 19:32-71.

Harig, A. L., K. D. Fausch, and M. K. Young. 2000. Factors influencing success of greenback cutthroat trout translocations. North American Journal of Fisheries Management 20:994-1004.

Hilderbrand, R. H. 2003. The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. Biological Conservation 110:257-266.

Hollender, B. A., and R. F. Carline. 1994. Injury to wild brook trout by backpack electrofishing. North American Journal of Fisheries Management 14:643-649.

Hughes, N. F., and T. C. Grand. 2000. Physiological ecology meets the ideal-free distribution: predicting the distribution of size-structured fish populations across temperature gradients. Environmental Biology of Fishes 59:285-298.

Jonsson, B., N. Jonsson, K. Hindar, T. G. Northcote, and S. Engen. 2008. Asymmetric competition drives lake use of coexisting salmonids. Oecologia 157:553-560.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L., and *S. trutta* L.). Institute of Freshwater Research Drottningholm 39:55-98.

Kebus, M. J., M. T. Collins, M. S. Brownfield, C. H. Amundson, T. B. Kayes, and J. A. Malison. 1992. Effects of rearing density on the stress response and growth of rainbow trout. Journal of Aquatic Animal Health 4:1-6.

Koenig, M. K. 2006. Habitat and biotic factors influencing the distribution and recruitment of juvenile cutthroat trout in the Teton River, Idaho. Master's thesis. Utah State University, Logan.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16:199-204.

Krueger, C. C., and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48:66-77.

Liknes, G. A., and P. J. Graham. 1988. Westslope cutthroat trout in Montana: life history, status, and management. American Fisheries Society Symposium 4:53-60.

MacPhee, C. 1966. Influence of differential angling mortality and stream gradient on fish abundance in a trout-sculpin biotope. Transactions of the American Fisheries Society 95:381-387.

McGrath, C. C., and W. M. Lewis. 2007. Competition and predation as mechanisms for displacement of greenback cutthroat trout by brook trout. Transactions of the American Fisheries Society 136:1381-1392.

McHugh, P., and P. Budy. 2006. Experimental effects of nonnative brown trout on the individual- and population-level performance of native Bonneville cutthroat trout. Transactions of the American Fisheries Society 135:1441-1455.

McHugh, P., P. Budy, G. Thiede, and E. Vandyke. 2008. Trophic relationships of nonnative brown trout, *Salmo trutta*, and native Bonneville cutthroat trout, *Oncorhynchus clarkii utah*, in a northern Utah, USA river. Environmental Biology of Fishes 81:63-75.

McIntyre, J. D., and B. E. Rieman. 1995. Westslope cutthroat trout. Pages 1-15 *in* M. K. Young, technical editor. Conservation assessment for inland cutthroat trout, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

McMichael, G. A. 1993. Examination of electrofishing injury and short-term mortality in hatchery rainbow trout. North American Journal of Fisheries Management 13:229-233.

McQuarrie, A. D. R., and C. L. Tsai. 1998. Regression and time series model selection. World Scientific, River Edge, New Jersey.

Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fishes during the past century. Fisheries 14(6):22-38.

Nakano, S., and T. Furukawa-Tanaka. 1994. Intra- and interspecific dominance hierarchies and variation in foraging tactics of two species of stream-dwelling chars. Ecological Research 9:9-20.

Newman, M. A. 1956. Social behavior and interspecific competition in two trout species. Physiological Zoology 29:64-81.

Nielsen, J. L. 1998. Scientific sampling effects: electrofishing California's endangered fish populations. Fisheries 23(12):6-12.

Novinger, D. C. 2000. Reversals in competitive ability: do cutthroat trout have a thermal refuge from competition with brook trout? Doctoral dissertation. University of Wyoming, Laramie.

Peterson, D. P., and K. D. Fausch. 2003. Testing population-level mechanisms of invasion by a mobile vertebrate: a simple conceptual framework for salmonids in streams. Biological Invasions 5:239-259.

Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of brook trout on native cutthroat trout. Ecological Applications 14:754-772.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and the R Core team. 2008. nlme: linear and nonlinear mixed effects models. R package version 3.1-89, R Foundation for Statistical Computing, Vienna. Available: http://CRAN.R-project.org/package=nlme (October 2008).

Pope, K. L., and C. G. Kruse. 2007. Condition. Pages 423-472 *in* C. S Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. Available: http://CRAN.R-project.org (October 2009).

Reinthal, P. N., and M. L. J. Stiassny. 1991. The freshwater fishes of Madagascar: a study of an endangered fauna with recommendations for a conservation strategy. Conservation Biology 5:231-243.

Reynolds, J. B., A. L. Kolz, N. G. Sharber, and S. W. Carothers. 1988. Electrofishing injury to large rainbow trout. North American Journal of Fisheries Management 8:516-518.

Riley, S. C., and K. D. Fausch. 1992. Underestimation of trout population size by maximum-likelihood removal estimates in small streams. North American Journal of Fisheries Management 12:768-776.

Ripley, B. 2010. Package 'Mass': main package of Venables and Ripleys MASS. Available: http://www.stats.ox.ac.uk/pub/MASS4/ (January 2010).

Rose, G. A. 1986. Growth decline in subyearling brook trout (*Salvelinus fontinalis*) after emergence of rainbow trout (*Salmo gairdneri*). Canadian Journal of Fisheries and Aquatic Sciences 43:187-193.

Rosenfeld, J. S., and J. Taylor. 2009. Prey abundance, channel structure and the allometry of growth rate potential for juvenile trout. Fisheries Management and Ecology 16:202-218.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. MacMillan USA, New York.

Schill, D. J., and F. S. Elle. 2000. Healing of electroshock-induced hemorrhages in hatchery rainbow trout. North American Journal of Fisheries Management 20:730-736.

Schwarz, G. 1978. Estimating the dimension of a model. Annals of Statistics 6:461-464.

Sharber, N. G., and S. W. Carothers. 1988. Influence of electrofishing pulse shape on spinal injuries in adult rainbow trout. North American Journal of Fisheries Management 8:117-122.

Shemai, B., R. Sallenave, and D. E. Cowley. 2007. Competition between hatchery-raised Rio Grande cutthroat trout and wild brown trout. North American Journal of Fisheries Management 27:315-325.

Shepard, B. B., B. E. May, and W. Urie. 2005. Status and conservation of westslope cutthroat trout within the western United States. North American Journal of Fisheries Management 25:1426-1440.

Shepard, B. B., B. Sanborn, L. Ulmer, and D. C. Lee. 1997. Status and risk of extinction for westslope cutthroat trout in the upper Missouri River Basin, Montana. North American Journal of Fisheries Management 17:1158-1172.

Shepard, B. B., K. L. Pratt, and P. J. Graham. 1984. Life histories of westslope cutthroat and bull trout in the upper Flathead River Basin, Montana. Report of Montana Department of Fish, Wildlife and Parks to U.S. Environmental Protection Agency, Contract Number R008224-01-5, Helena.

Shepard, B. B., R. Spoon, and L. Nelson. 2002. A native westslope cutthroat trout population responds positively after brook trout removal and habitat restoration. Intermountain Journal of Sciences 8:191-211.

Spens, J., A. Alanara, and L. O. Eriksson. 2007. Nonnative brook trout (*Salvelinus fontinalis*) and the demise of native brown trout (*Salmo trutta*) in northern boreal lakes: stealthy, long-term patterns? Canadian Journal of Fisheries and Aquatic Sciences 64:654-664.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union 38:913-920.

SYSTAT. 2004. SYSTAT 11. SPSS Incorporated, Chicago.

Thomas, H. M. 1996. Competitive interactions between native and exotic trout species in a high mountain stream. Master's thesis. Utah State University, Logan.

Townsend, C. R. 1996. Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. Biological Conservation 78:13-22.

Van Deventer, J. S., and W. S. Platts. 1989. Microcomputer software system for generating population statistics from electrofishing data - User's guide for Microfish 3.0. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, General Technical Report INT-254, Ogden, Utah.

White, G. C., D. R. Anderson, K. P. Burnham and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. U.S. Department of Energy, Los Alamos National Laboratory, Report LA-8787-NERP, Los Alamos, New Mexico.

Young, K. A. 2003. Evolution of fighting behavior under asymmetric competition: an experimental test with juvenile salmonids. Behavioral Ecology 14:127-134.

Young, K. A. 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. Ecology 85:134-149.

Zimmerman, J. K. H., and B. Vondracek. 2006. Effects of stream enclosures on drifting invertebrates and fish growth. Journal of the North American Benthological Society 25:453-464.

Table 4.1. Physical characteristics of three Rocky Mountain streams where westslope cutthroat trout response to brook trout removals was evaluated from 1993 through 2007.

	Stream		
Parameter	Cottonwood	Muskrat	Whites
Elevation range (m)	970-1830	1480-2350	1200-1870
Elevation range of treatment reach (m)	1590-1780	1920-2100	1600-1790
Length of stream (km)	31.1	33.9	25.5
Treatment length (km)	3.0	2.3	2.9
Wetted width (m)	2.4	2.6	2.0
Stream order[1]	3rd	3rd	3rd
Channel gradient (%)	6	6	3
Late summer discharge (m^3/sec)	0.10	0.17	0.08
Water temperature (C)	12-17	6-16	8-10
Conductivity (µmhos)	88	72	660
pH	8.7	8.4	8.2
Riparian vegetation (density - and predominant types)	Sparse – willow, aspen	Moderate – conifer, alder	Moderate – willow, alder

[1] Strahler (1957)

Table 4.2. Length-weight regression model results (log_{10}-length versus log_{10}-weight) for all westslope cutthroat trout that were captured and weighed in treatment reaches of Cottonwood, Muskrat, and Whites creeks from 1993 through 2007 showing number of years sampling occurred, total number of fish used in regression analyses (n), and estimates of intercept, slope, adjusted R^2, mean square error (*MSE*), variance of the intercept, covariance, and variance of slope.

Stream	Years	n	Intercept	Slope	Adj-R^2	*MSE*	Variance of intercept	Covariance	Variance of slope
Cottonwood	4	985	-5.130	3.042	0.985	0.00200	0.00063	-0.00030	0.00014
Muskrat	10	869	-5.001	2.995	0.976	0.00400	0.00110	-0.00053	0.00025
Whites	15	2262	-5.177	3.070	0.981	0.00378	0.00035	-0.00017	0.00008

Table 4.3. Spearman rank correlation coefficients (bold values indicate significance at $P < 0.05$) for conditions and densities of juvenile and adult westslope cutthroat trout (WCT), densities of juvenile and adult brook trout, whether densities were estimated the same year or the previous year, and deviations of average annual air temperatures and average annual discharge estimates from long-term averages.

Parameter	Density of WCT juveniles	Density of WCT adults	Condition of WCT juveniles	Condition of WCT adults
Condition of WCT juveniles	-0.175	-0.065	**---**	**0.777**
Condition of WCT adults	**-0.410**	-0.234	**0.777**	**---**
Density of WCT juveniles	**---**	**0.6018**	-0.175	**-0.410**
Density of WCT adults	**0.602**	**---**	-0.065	-0.234
Density of brook trout juveniles	**-0.631**	**-0.535**	-0.137	0.092
Density of brook trout adults	**-0.538**	**-0.352**	-0.145	0.117
Previous year density of WCT adults	**0.432**	**-0.477**	-0.083	-0.284
Previous year density of brook trout juveniles	**-0.605**	-0.292	-0.266	-0.196
Previous year density of brook trout adults	**-0.614**	0.351	-0.323	-0.156
Annual air temperature deviation from mean	-0.038	**-0.495**	-0.091	-0.248
Annual discharge deviation from mean	**-0.523**	**-0.370**	0.254	**0.410**

Table 4.4. Negative binomial regression analyses showing the effects of juvenile and adult fish densities (number/hectare; WCT = westslope cutthroat trout; BT = brook trout) on estimated numbers of juvenile westslope cutthroat trout. Sample area (m^2) was entered as an offset. Coefficient values are shown for the best models determined by corrected Akaike Information Criterion (AIC*c*; lower values indicate better models). Bold coefficient values indicate significance at $P < 0.05$. Standard errors of coefficient estimates are shown in parentheses below coefficients.

Covariate	Estimated coefficient (S.E.)				
Intercept	**-5.6234**	**-5.4786**	**-6.4347**	**-5.5083**	**-5.1666**
	(0.7461)	(0.8152)	(0.6732)	(0.8238)	(1.0291)
log(WCT adult density)	**0.6066**	**0.5668**	**0.6935**	**0.5815**	**0.5213**
	(0.1251)	(0.1360)	(0.1251)	(0.1412)	(0.1775)
log(Brook trout juvenile density)		**-0.1312**		-0.0671	-0.1842
		(0.0598)		(0.1306)	(0.2355)
log(Brook trout adult density)	**-0.1468**			-0.0784	-0.0955
	(0.0618)			(0.1349)	(0.1422)
BT juvenile X WCTadult					0.0271
					(0.0492)
<u>Regression statistics</u>					
AIC*c*	329.71	329.72	331.72	332.37	334.45
delta AIC*c*		0.01	2.01	2.66	4.74
Residual deviance	32.85	32.84	33.30	32.83	32.81
Residual degrees of freedom	27	27	28	26	25

The expected value for the density of juvenile cutthroat is:

$$E(density) = e^{\beta_0} * e^{\beta_1 \log n(WCT\ adult\ density)} * e^{\beta_2 \log n(BT\ adult\ density)} * e^{\beta_3 \log n(BT\ juvenile\ density)},$$

where β-values are the estimated coefficients and $\log_n$(Area) is added to the intercept.

Table 4.5. Negative binomial regression analyses showing the effects of juvenile and adult fish densities (number/hectare; WCT = westslope cutthroat trout; BT = brook trout) on estimated numbers of adult westslope cutthroat trout. Sample area (m^2) was entered as an offset. Coefficient values are shown for the best models determined by the corrected Akaike Information Criterion (AIC*c*; lower values indicate better models). Bold coefficient values indicate significance at $P < 0.05$. Standard errors of coefficient estimates are shown in parentheses below coefficients.

Covariate	Estimated coefficient (S.E.)				
Intercept	**-6.1505**	**-6.1496**	**-6.6198**	**-5.7344**	**-6.8734**
	(0.8763)	(0.8776)	(0.6920)	(0.9540)	(0.9437)
log(WCT juvenile density)	**0.4205**	**0.4205**	**0.5005**	**0.3927**	**0.5300**
	(0.1252)	(0.1252	(0.1117)	(0.1374)	(0.13356)
log(Brook trout juvenile density)	**-0.3727**	-0.3751		-0.0977	
	(0.1134)	(0.2082)		(0.0664)	
log(Brook trout adult density)	**0.3250**	**0.3242**			0.0271
	(0.1210)	(0.1262)			(0.0727)
BT juvenile X BT adult		0.0006			
		(0.0372)			
Regression statistics					
AIC*c*	280.57	283.72	283.96	284.92	286.50
delta AIC*c*		3.15	3.39	4.35	5.93
Residual deviance	31.77	31.77	32.98	32.71	32.97
Residual d.f.	26	25	28	27	27

The expected value for the density of adult cutthroat is:

$$E(density) = e^{\beta_0} * e^{\beta_1 \log n(WCT\ juvenile\ density)} * e^{\beta_2 \log n(BT\ adult\ density)} * e^{\beta_3 \log n(BT\ juvenile\ density)},$$

where β-values are the estimated coefficients and $\log_n$(Area) is added to the intercept.

Table 4.6. Results of non-linear mixed-effects model for Whites Creek showing estimated coefficients for westslope cutthroat trout (a) and brook trout (b), breadth of competition by species (WCT = westslope cutthroat trout; BT = brook trout), estimated asymmetry coefficient (NA indicates "not applied"), standard deviation (S.D.) of year effect and residual, Bayesian information criteria (BIC), difference in BIC from best model, and model log likelihood. Models are shown in order from lowest (left column) to highest (right column) BIC ranking. Bold coefficients indicate significance $P < 0.05$ and italicized coefficients indicate significance $P < 0.10$. Standard errors of model parameter estimates shown under each estimate in parentheses. The top five models are shown.

Whites Creek	a (WCT)=b (BT) WCT=BT breadth no asymmetry	a (WCT)=b (BT) WCT=BT breadth = asymmetry	a (WCT)<>b (BT) WCT=BT breadth no asymmetry	a (WCT)=b (BT) WCT<>BT breadth no asymmetry	a (WCT)<>b (BT) WCT<>BT breadth no asymmetry
a	**-0.000037**	**-0.000037**	**-0.000035**	**-0.000039**	**-0.000036**
	(0.000010)	(0.000010)	(0.000011)	(0.000010)	(0.000012)
b	**-0.000037**	**-0.000037**	-0.000051	**-0.000039**	-0.000048
	(0.000010)	(0.000010)	(0.000041)	(0.000010)	(0.000047)
WCT breadth	**0.436509**	**0.477235**	**0.433207**	**0.451466**	**0.453743**
	(0.129435)	(0.147194)	(0.130016)	(0.134193)	(0.153848)
BT breadth	**0.436509**	**0.477235**	**0.433207**	0.007560	-0.368449
	(0.129435)	(0.147194)	(0.130016)	(0.025893)	(0.452421)
Size-asymmetry	NA	0.2352	NA	NA	NA
		(0.2019)			
S.D. Year	0.0689	0.0695	0.0699	0.0666	0.0697
S.D. Residual	0.1253	0.1252	0.1253	0.1253	0.1253
BIC	-2760.00	-2753.97	-2752.44	-2751.18	-2744.93
delta BIC	---	6.03	7.56	8.82	15.07
log likelihood	1395.35	1396.18	1395.41	1394.78	1395.49

Table 4.7. Results of non-linear mixed-effects model for Muskrat Creek showing estimated coefficients for westslope cutthroat trout (a) and brook trout (b), breadth of competition by species (WCT = westslope cutthroat trout; BT = brook trout), estimated asymmetry coefficient (NA indicates “not applied”), standard deviation (S.D.) of year effect and residual, Bayesian information criteria (BIC), difference in BIC from best model, and model log likelihood. Models are shown in order from lowest (left column) to highest (right column) BIC ranking. Bold coefficients indicate significance $P < 0.05$ and italicized coefficients indicate significance $P < 0.10$. Standard errors of model parameter estimates shown under each estimate in parentheses. The top five models are shown.

Muskrat Creek	a (WCT)=b (BT) WCT=BT breadth = asymmetry	a (WCT)<>b (BT) WCT=BT breadth = asymmetry	a (WCT)=b (BT) WCT=BT breadth no asymmetry	a (WCT)<>b (BT) WCT=BT breadth no asymmetry	a (WCT)=b (BT) WCT<>BT breadth no asymmetry
a	*-0.000029*	0.000080	*-0.0000159*	-0.0000077	-0.0000173
	(0.000016)	(0.000013)	(0.0000096)	(0.0000105)	(0.0000110)
b	*-0.000029*	-0.000017	*-0.0000159*	-0.0000375	-0.0000173
	(0.000016)	(0.000030)	(0.0000096)	(0.0000236)	(0.0000110)
WCT breadth	**-0.182384**	**0.079529**	-0.3774067	0.2854423	0.4133052
	(0.061261)	(0.34601)	(0.3340215)	(0.2771920)	(0.3768360)
BT breadth	**-0.182384**	**0.079529**	-0.3774067	0.2854423	-0.2594392
	(0.061261)	(0.34601)	(0.3340215)	(0.2771920)	(0.5743981)
Size-asymmetry	-4.4020	18.6949	NA	NA	NA
	(3.1295)	(16.2461)			
S.D. Year	0.06999	0.05112	0.05444	0.05230	0.05558
S.D. Residual	0.13283	0.13320	0.13474	0.13472	0.13471
BIC	-1571.69	-1563.15	-1545.09	-1539.05	-1538.05
delta BIC	---	8.55	26.60	32.64	33.64
log likelihood	803.90	803.24	786.99	787.58	787.08

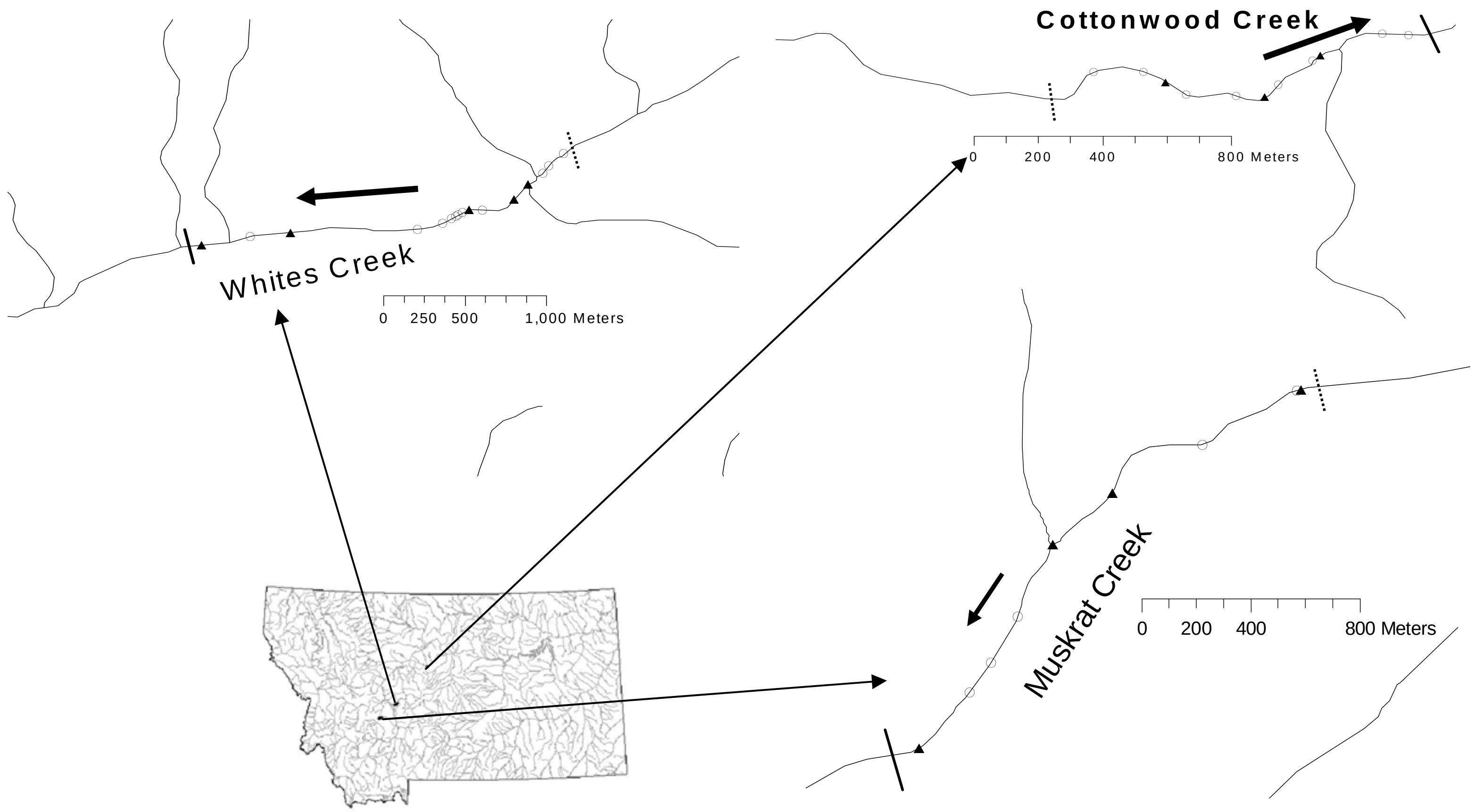


Figure 4.1. Maps of study streams showing their location in Montana, lower barriers (dark solid lines), extents of brook trout removal treatments (barrier up to dotted line), and locations of sample sections (dark triangles are long-term estimate sections and open circles are other sample sections) within treatment reaches. Flow direction is indicated by arrows.

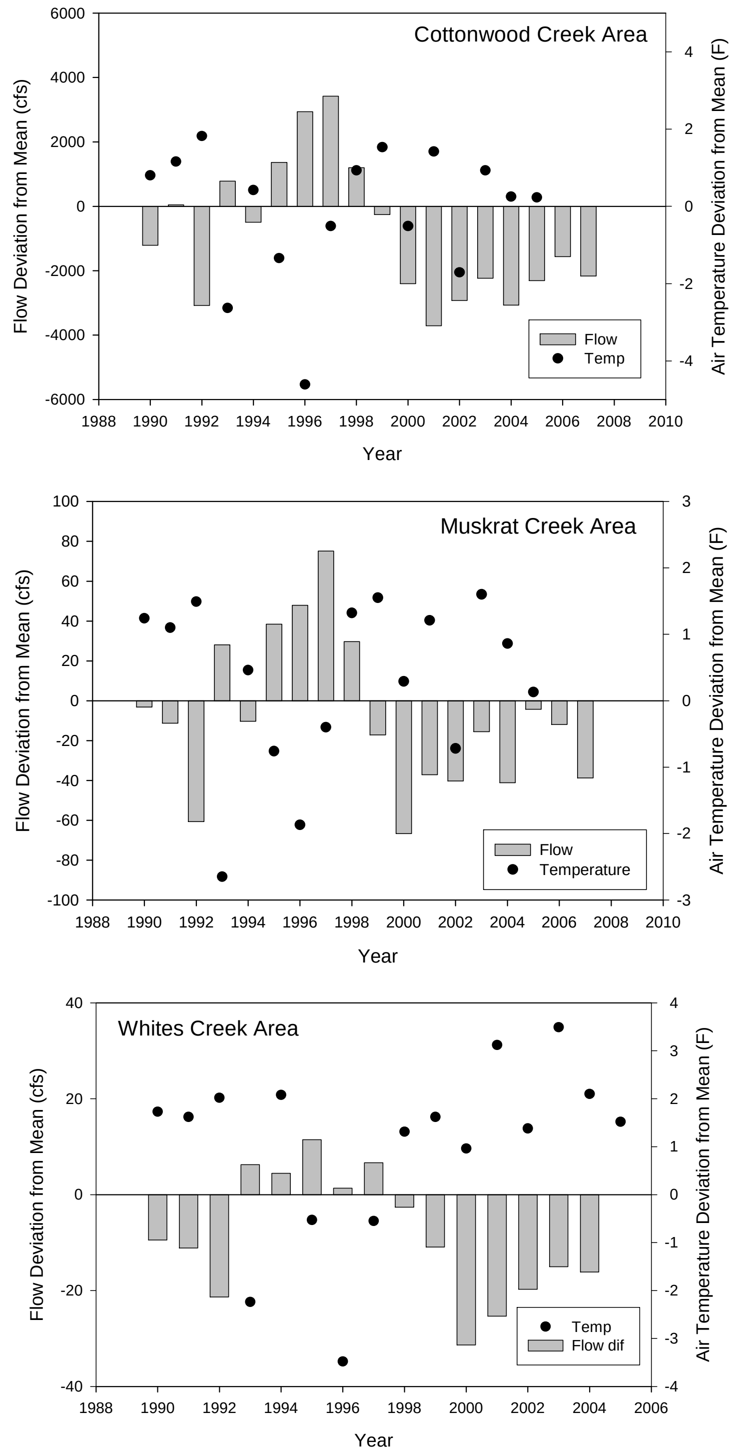


Figure 4.2. Annual discharge and temperature deviations from historical means for 1990 through 2007 for sites near sample streams.

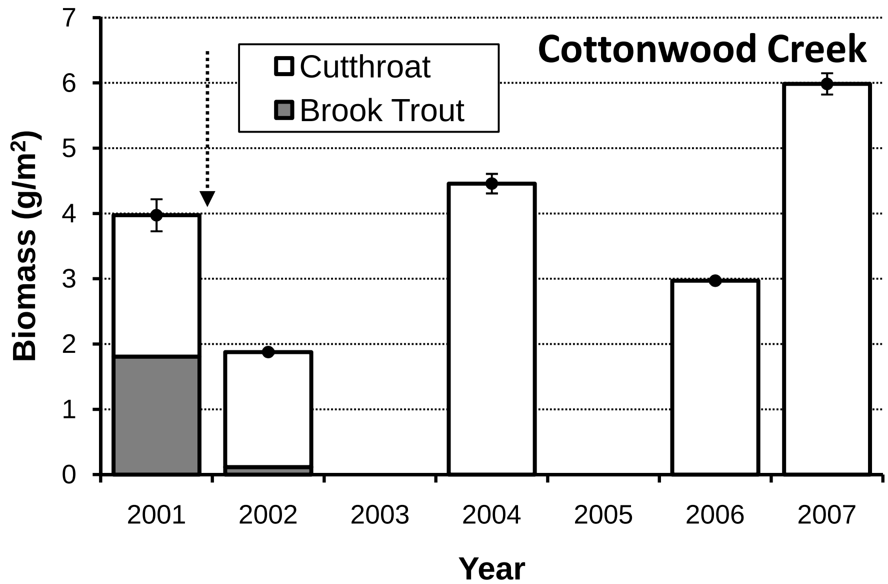


Figure 4.3. Biomass estimates (g/m^2) of westslope cutthroat trout (Cutthroat) and brook trout 75 mm and longer by year averaged over all sample sections within the treatment reaches of Cottonwood Creek where brook trout were removed. Total biomass estimates (black solid circles) and associated 95% CIs (vertical capped lines) are shown at top of bars. Vertical dotted arrow indicates when brook trout removals began.

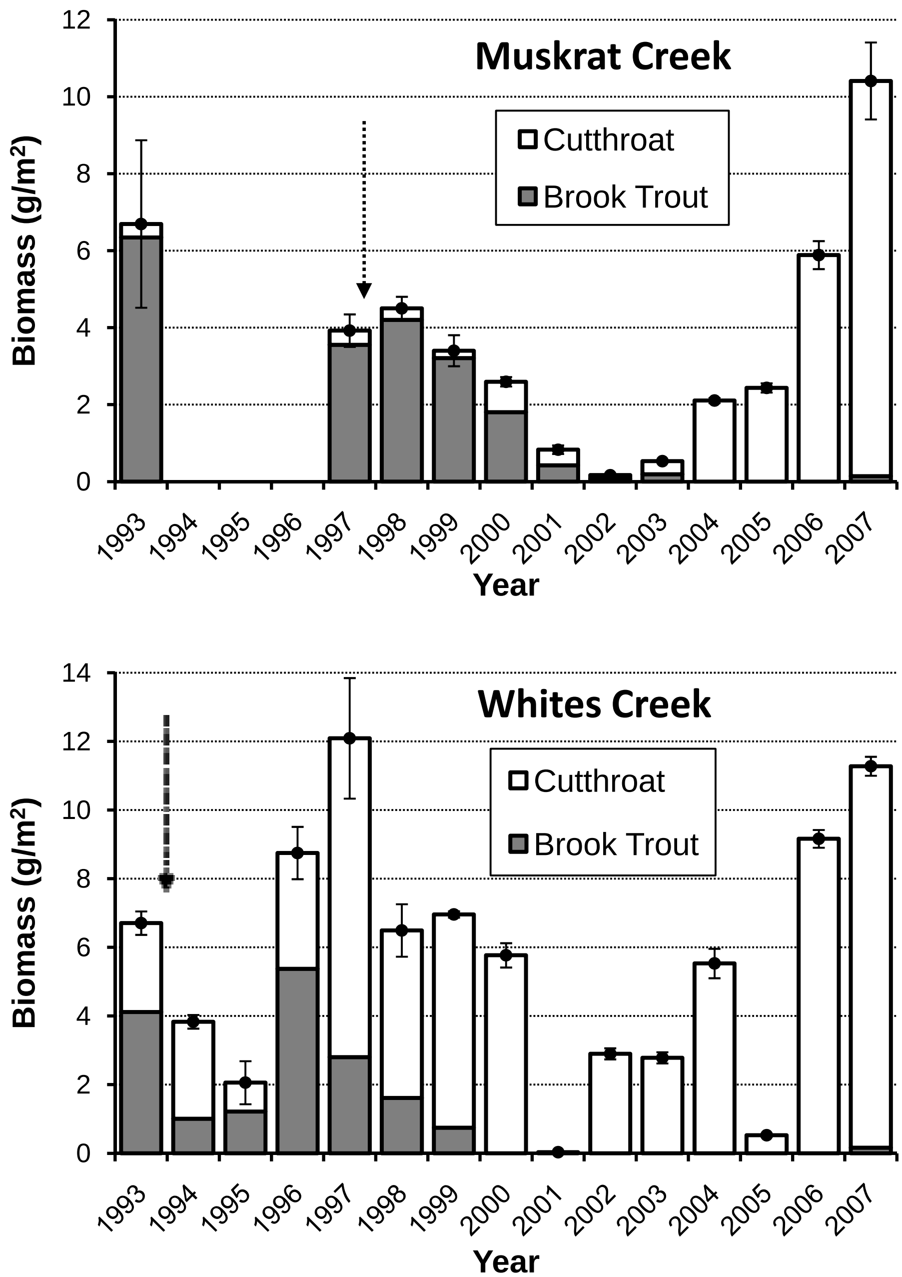


Figure 4.4. Biomass estimates (g/m^2) of westslope cutthroat trout (Cutthroat) and brook trout 75 mm and longer by year averaged over all sample sections within the treatment reaches of Muskrat (top) and Whites (bottom) creeks where brook trout were removed. Total biomass estimates (black solid circles) and associated 95% CIs (vertical capped lines) are shown at top of bars. Vertical dotted arrows indicate when brook trout removals began. Wider 95% CIs for the Muskrat 1993 resulted because only one section was sampled.

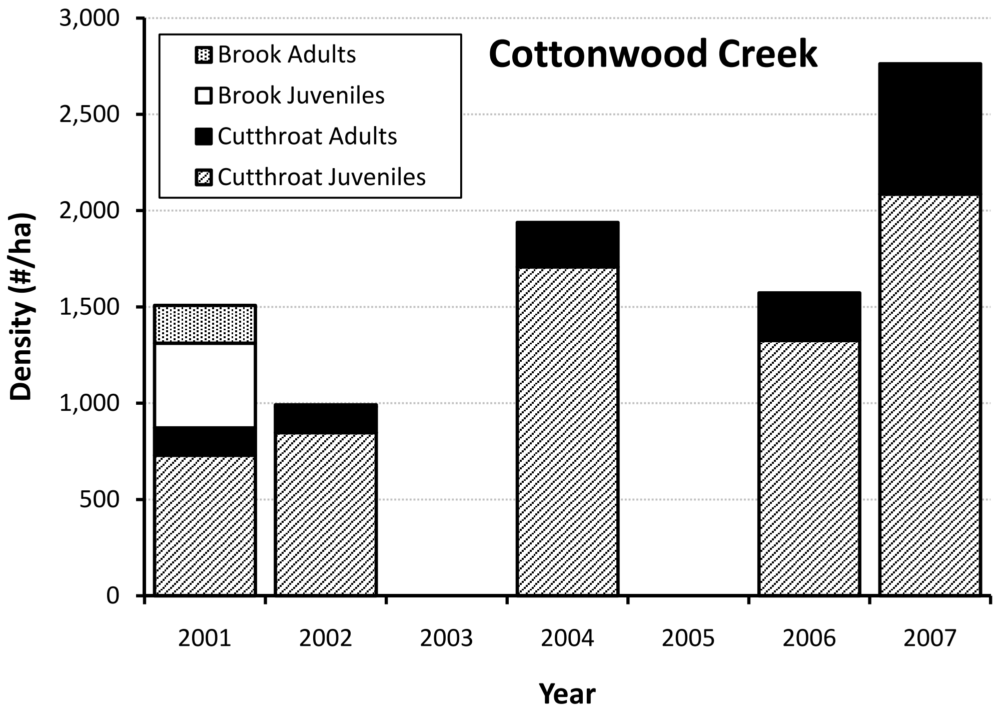


Figure 4.5. Densities of juvenile (75 to 149 mm) and adult ($\geq$ 150 mm) westslope cutthroat trout (Cutthroat) and brook trout (Brook) estimated in reaches where brook trout were removed in Cottonwood Creek. Estimates were not made in years lacking bars (2003 and 2005).

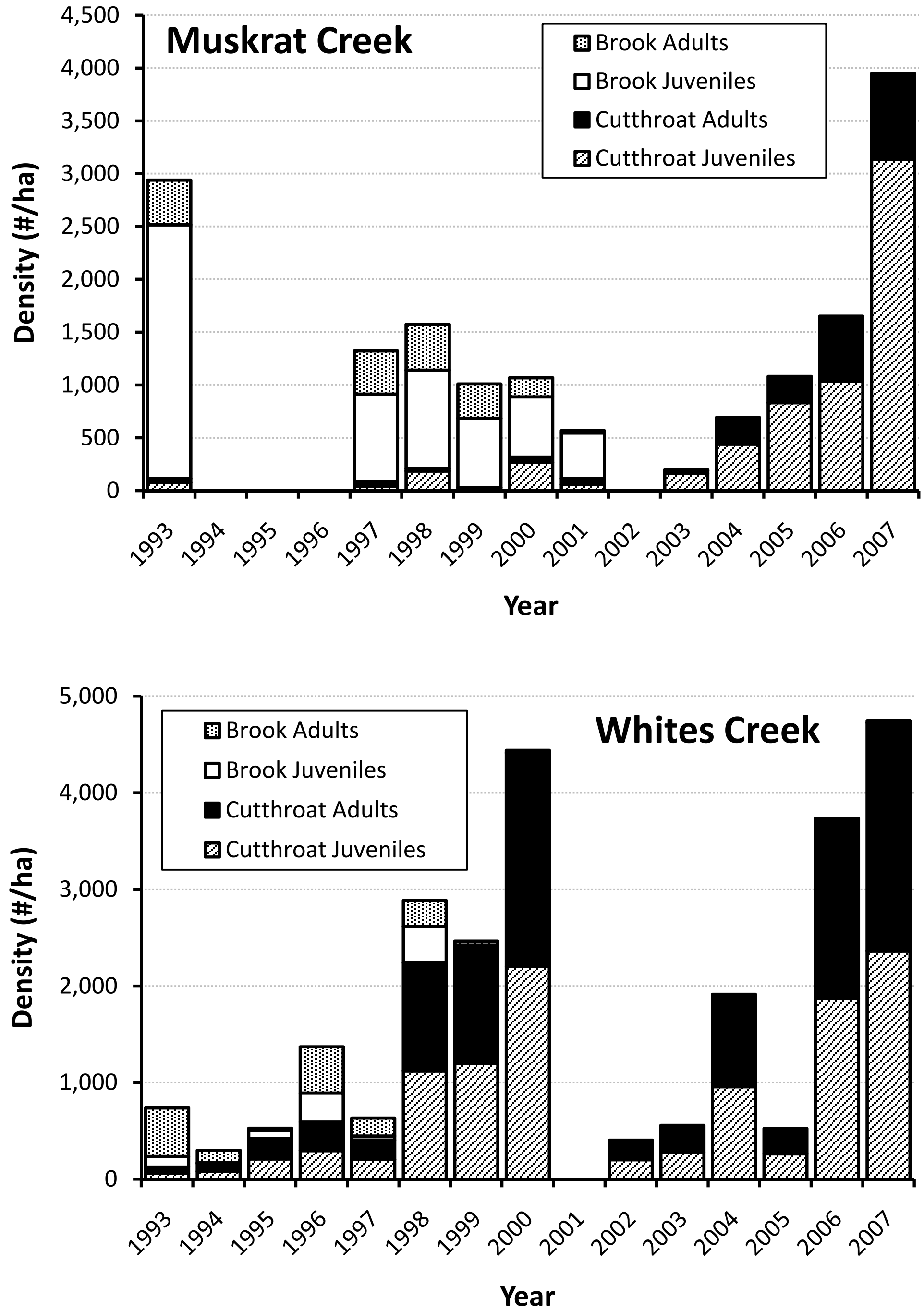


Figure 4.6. Densities of juvenile (75 to 149 mm) and adult ($\geq$ 150 mm) westslope cutthroat trout (Cutthroat) and brook trout (Brook) estimated in reaches where brook trout were removed in Muskrat (top) and Whites (bottom) creeks. Estimates were not made in years lacking bars.

CHAPTER 5

SYNTHESIS AND CONCLUSIONS

My research focused on determining whether nonnative brook trout occupied a niche similar to that of native westslope cutthroat trout in headwater mountain streams of the Northern Rocky Mountains. I wanted to find out if brook trout competitively excluded westslope cutthroat trout from headwater stream habitats. This research has important implications for the conservation of native cutthroat trout. If brook trout and cutthroat trout occupy a similar niche, especially if it can be shown that brook trout competitively exclude cutthroat trout, then conservation of cutthroat trout will require physically excluding brook trout from cutthroat trout conservation areas. Conversely, if these two species occupy separate niches, or if neither species has a distinct competitive advantage, then the presence and expansion of brook trout into waters occupied by native cutthroat trout should pose much less risk to these cutthroat trout populations.

To accomplish my objectives I first evaluated and further developed depletion population estimators for estimating population abundances and biomasses (Chapter 2). I demonstrated that depletion population estimators were biased, but that deviation of population estimates from true population size was not a major problem if a relatively high proportion (> 70%) of the estimated population was captured. This is a convenient method that can be used to evaluate potential bias. Fortunately, in small streams biologists often capture a high proportion of the estimated population during depletion population estimates, making bias less of a concern.

I incorporated a finite population correction factor methodology that dramatically improved the precision of biomass estimates and provided confidence intervals that were much closer to the desired nominal level compared to the method currently used. I showed that two different finite population correction factors (an *a priori* sampling design estimator and an *a posteriori* model-based estimator) provided the same results. I recommend the model-based method because it is more flexible by allowing variance to be partitioned into different components. This improved biomass estimator will allow fisheries biologists to better detect significant changes in fish populations in small streams.

Next, I implemented and evaluated repeated electrofishing to eradicate brook trout from relatively long reaches of headwater streams. I did this as a treatment to evaluate the response of westslope cutthroat trout before, during, and after the eradication of brook trout in a wild setting and to conserve extant populations of westslope cutthroat trout. I was able to successfully eradicate brook trout from relatively long reaches of four streams and demonstrated for the first time that electrofishing can be used to eradicate nonnative trout from headwater streams in the Rocky Mountain West. I determined that electrofishing cannot be used to eradicate trout from larger streams (> 6 m wide) or from smaller streams that have dense cover or beaver ponds. I learned several strategies that increased the probability and efficiency of eradication by electrofishing and share that information so that conservation biologists can adopt these strategies when conducting electrofishing eradication projects.

I was able to provide compelling evidence that brook trout and westslope cutthroat trout occupy a similar niche and that brook trout competitively excluded westslope cutthroat from my three headwater study streams. The significant increase in total fish biomass after the eradication of brook trout suggests that both interference and exploitive competition occurs between these two species. The perception that brook trout can have significant effects on cutthroat trout populations appears to be warranted, at least in the upper Missouri River drainage.

Implications for Conservation of Cutthroat Trout

Brook trout usually displace cutthroat trout where they are able to invade. Maintaining native cutthroat trout populations in tributaries where brook trout might invade will require physical barriers to prevent invasion (Chapter 3; Novinger and Rahel 2003; Wofford et al. 2005; Van Houdt et al. 2005; Peterson et al. 2008). If brook trout invade habitats occupied by cutthroat trout, these brook trout can be eradicated using repeated electrofishing removals if the streams are small (< 4 m wetted width) and a barrier is constructed at the lower boundary of the treatment area (Chapter 3). Unfortunately, electrofishing eradication requires a barrier and will only work in small streams. These headwater areas above fish barriers may not provide enough stream habitat to allow native cutthroat trout populations to persist for long periods of time without human intervention (Shepard et al. 1997; Harig et al. 2000; Hilderbrand and Kershner 2000; Kruse et al. 2001; Harig and Fausch 2002; Hilderbrand 2002; Hilderbrand 2003; Shepard et al. 2005; Peterson et al. 2008; Fausch et al. 2009).

I suggest that a wide range of integrated conservation measures will be needed to conserve cutthroat trout. In locations where no nonnative trout occur, large areas of interconnected habitats that support cutthroat trout populations should be maintained. These conservation areas should be as large as possible to 1) protect as wide a diversity of life histories (i.e., migratory and resident) as possible, 2) include both lotic and lentic habitats, and 3) allow metapopulation dynamics to operate (e.g., Rieman and Dunham 2000). Where nonnative trout occur, cutthroat trout populations will need to be isolated to conserve their genetic integrity and prevent invasion by nonnative competitors that can displace them. Isolation of populations will require replication of many of these isolated populations to protect their genetic legacies and allow for re-founding of these populations should they be extirpated. Isolation may also require periodic genetic infusion to avoid inbreeding depression (genetic rescue; e.g., Schonhuth et al. 2003; Letcher et al. 2007; Zajitschek et al. 2009).

Recommendations for Future Research

I demonstrated that brook trout competitively excluded westslope cutthroat trout from headwater streams in the upper Missouri River basin, but this finding may not apply to streams west of the Continental Divide. Similar research should be done there. A result similar to mine would strengthen competitive exclusion inference. Similar studies should also be done to evaluate the effects of brook trout on other cutthroat trout subspecies to determine if different subspecies are affected differently by brook trout.

Perhaps physical setting mediates the effects of brook trout on cutthroat trout. I recommend finding places where westslope cutthroat trout appear to be resistant to invasion by brook trout or where these two species appear to co-exist and comparing flow and temperature regimes and physical habitat features to sites where brook trout are known to have displaced cutthroat trout to determine if these variables might mediate competition between these two species. Large-scale population and habitat data sets collected over wide geographic areas might provide insights into whether climatic, geographic, or geomorphic setting mediates or enhances displacement of cutthroat trout by brook trout.

Mechanisms by which brook trout exclude cutthroat trout should be further explored. I recommend examining how age-0 brook trout affect growth and condition of age-0 cutthroat trout, especially their condition immediately before the onset of winter as this is probably critical to their overwinter survival. More research is needed on the potential seasonal predation by brook trout on cutthroat trout especially during the late summer as young cutthroat trout emerge from their redds.

Literature Cited

Fausch, K. D., B. E. Rieman, J. B. Dunham, M. K. Young, and D. P. Peterson. 2009. Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. Conservation Biology 23:859-870.

Harig, A. L., and K. D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecological Applications 12:535-551.

Harig, A. L., K. D. Fausch, and M. K. Young. 2000. Factors influencing success of greenback cutthroat trout translocations. North American Journal of Fisheries Management 20:994-1004.

Hilderbrand, R. H. 2002. Simulating supplementation strategies for restoring and maintaining stream resident cutthroat trout populations. North American Journal of Fisheries Management 22:879-887.

Hilderbrand, R. H. 2003. The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. Biological Conservation 110:257-266.

Hilderbrand, R. H., and J. L. Kershner. 2000. Conserving inland cutthroat trout in small streams: how much stream is enough? Fisheries 20:513-520.

Letcher, B. H., K. H. Nislow, J. A. Coombs, M. J. O'Donnell, and T. L. Dubreuil. 2007. Population response to habitat fragmentation in a stream-dwelling brook trout population. Plos One. Available: http://www.plosone.org/article/info%3Adoi %2F10.1371%2Fjournal.pone.0001139 (April 2010).

Novinger, D. C., and F. J. Rahel. 2003. Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. Conservation Biology 17:772-781.

Peterson, D. P., B. E. Rieman, J. B. Dunham, K. D. Fausch, and M. K. Young. 2008. Analysis of trade-offs between threats of invasion by nonnative brook trout (*Salvelinus fontinalis*) and intentional isolation for native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). Canadian Journal of Fisheries and Aquatic Sciences 65: 557-573.

Rieman, B. E. and J. B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish 9:51-64.

Schonhuth, S., G. Luikart, and I. Doadrio. 2003. Effects of a founder event and supplementary introductions on genetic variation in a captive breeding population of the endangered Spanish killifish. Journal of Fish Biology 63:1538-1551.

Shepard, B. B., B. Sanborn, L. Ulmer, and D. C. Lee. 1997. Status and risk of extinction for westslope cutthroat trout in the upper Missouri River Basin, Montana. North American Journal of Fisheries Management 17:1158-1172.

Van Houdt, J. K. J., J. Pinceel, M. C. Flamand, M. Briquet, E. Dupont, F. A. M. Volckaert, and P. V. Baret. 2005. Migration barriers protect indigenous brown trout (*Salmo trutta*) populations from introgression with stocked hatchery fish. Conservation Genetics 6:175-191.

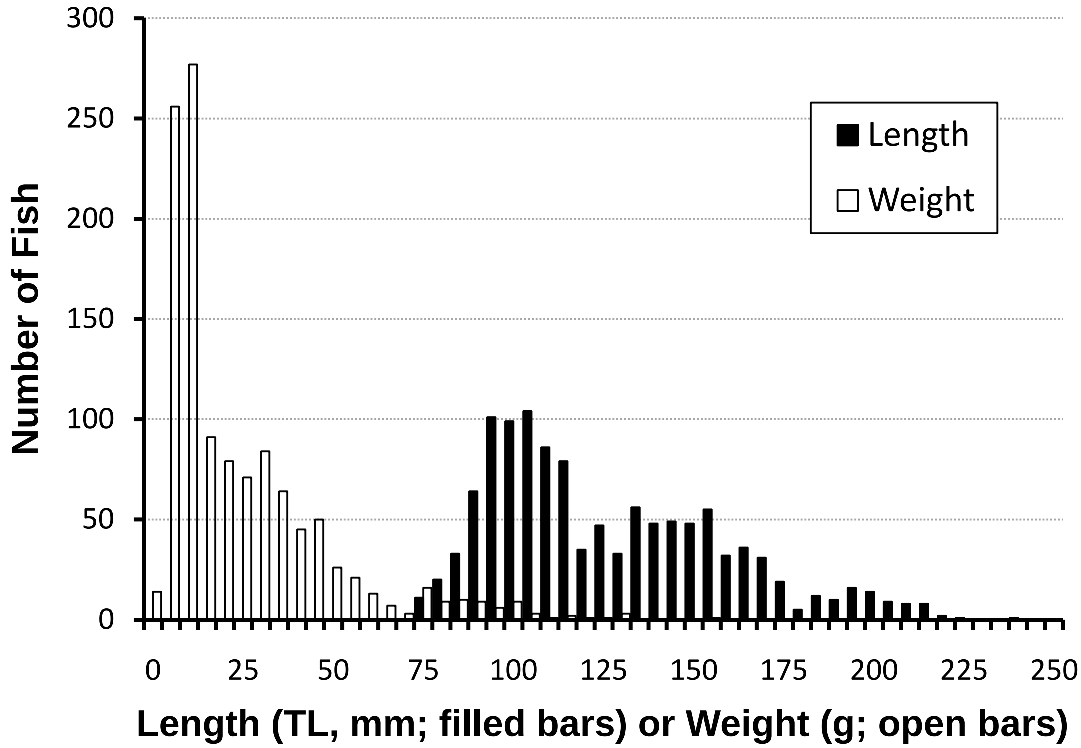
Wofford, J. E. B., R. E. Gresswell, and M. A. Banks. 2005. Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. Ecological Applications 15:628-637.

Zajitschek S. R. K., F. Zajitschek, and R.C. Brooks. 2009. Demographic costs of inbreeding revealed by sex-specific genetic rescue effects. BMC Evolutionary Biology 9:289.

APPENDICES

APPENDIX A

LENGTH AND WEIGHT DISTRIBUTIONS OF TROUT USED IN SIMULATIONS



A.1. Length and weight distribution of trout (brook trout) used for simulations.

APPENDIX B

BIAS IN REMOVAL POPULATION ESTIMATES FROM SIMULATION DATA

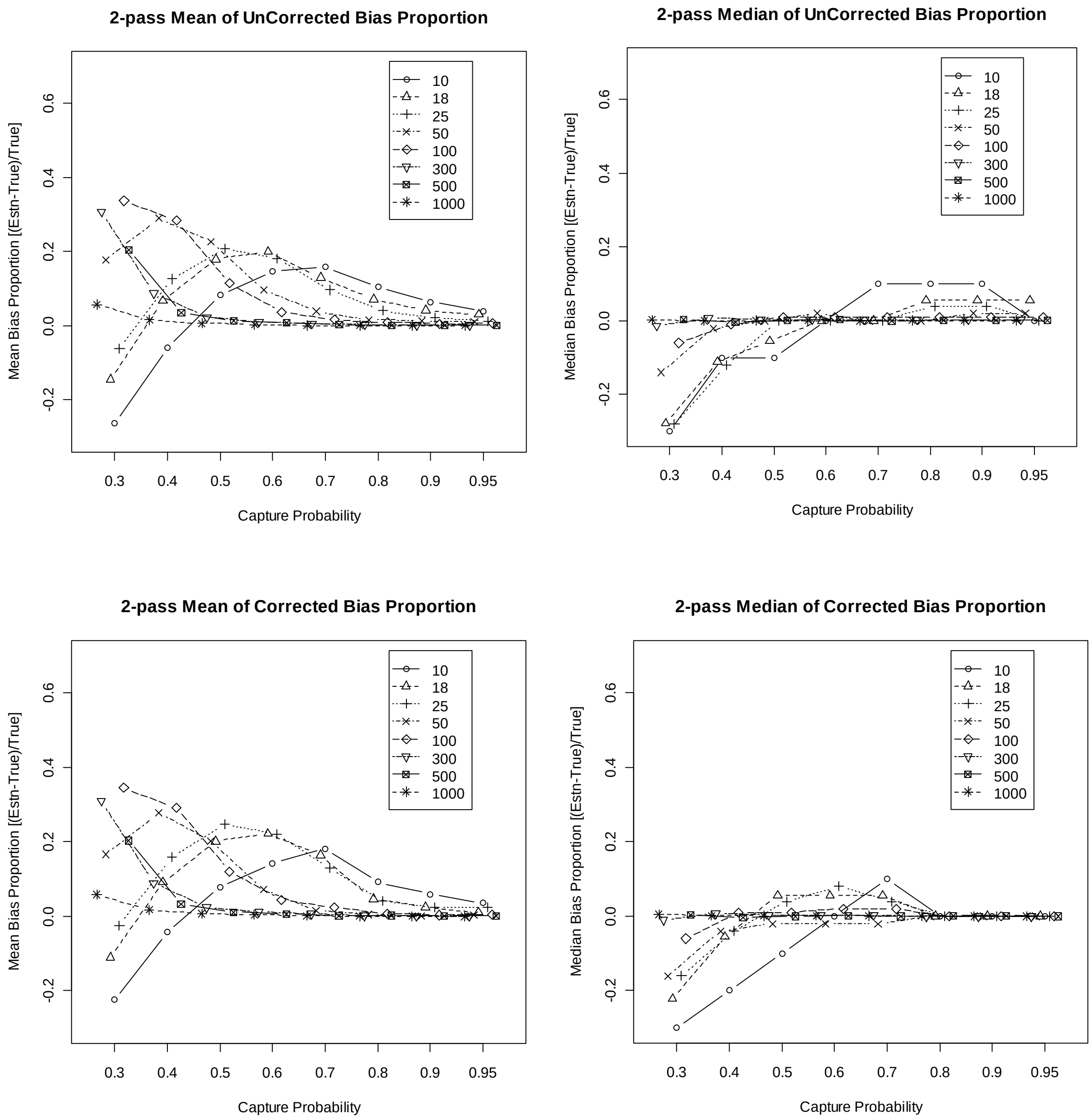


Figure B.1. Comparison of mean (left column) versus median (right column) proportional population estimate bias ([Estimate-True]/True) for two-removal uncorrected (top row) and bias-corrected (bottom row) population estimates by true capture probability (x-axis) and population size (different lines).

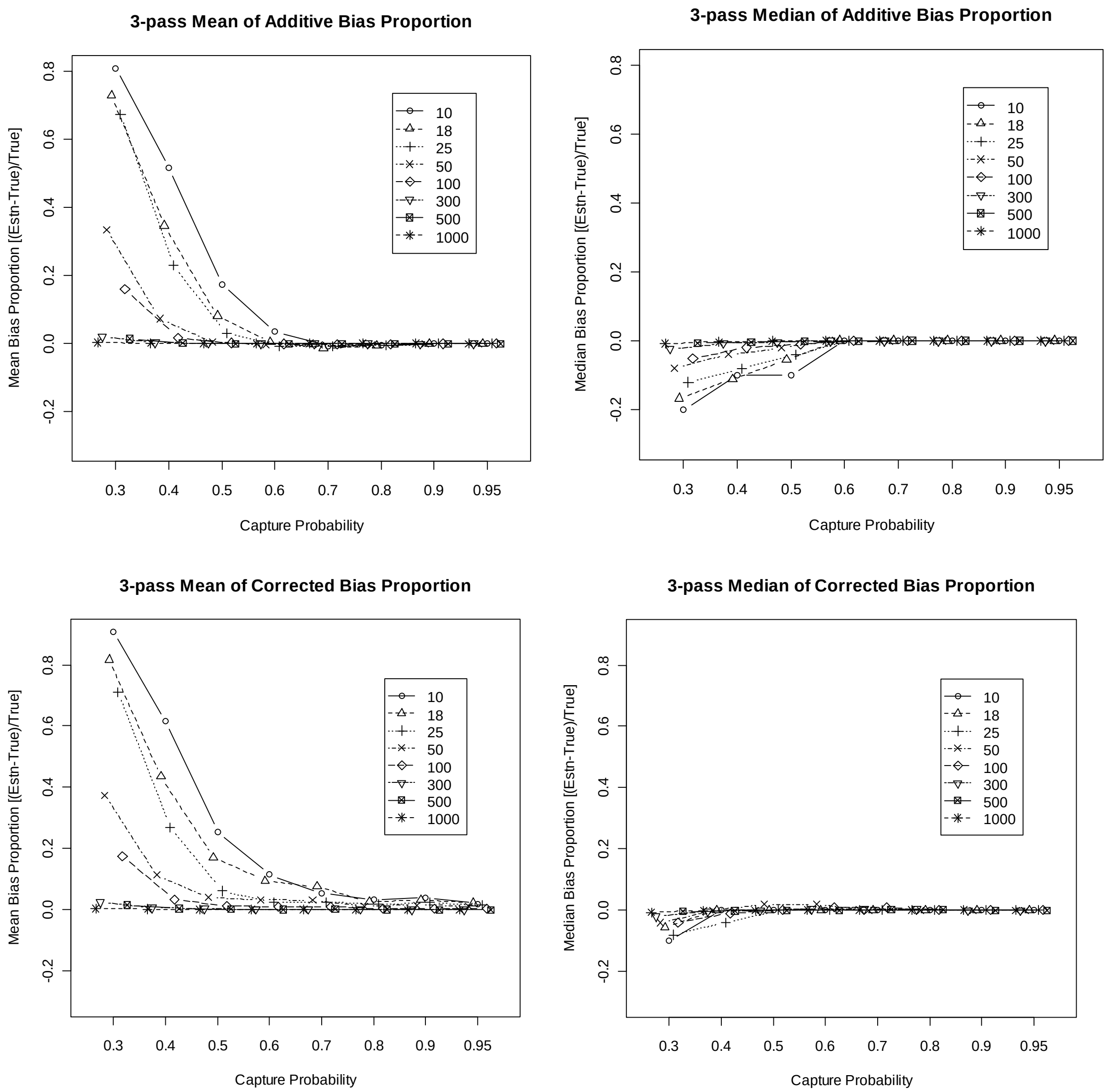


Figure B.2. Comparison of mean (left column) versus median (right column) proportional population estimate bias ([Estimate-True]/True) for three-removal uncorrected (top row) and bias-corrected (bottom row) population estimates by true capture probability (x-axis) and population size (different lines).

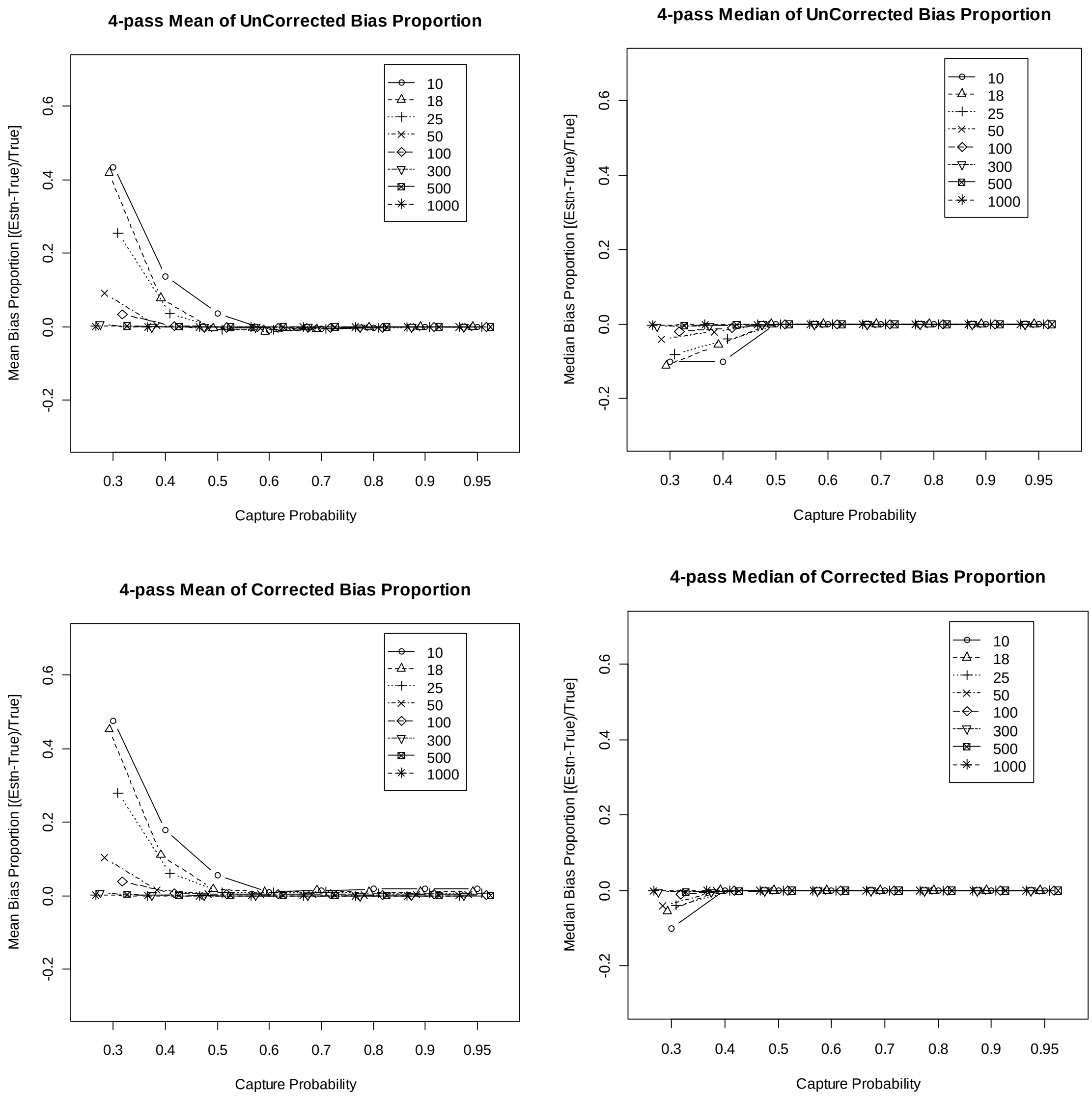


Figure B.3. Comparison of mean (left column) versus median (right column) proportional population estimate bias ([Estimate-True]/True) for four-removal uncorrected (top row) and bias-corrected (bottom row) population estimates by true capture probability (x-axis) and population size (different lines).

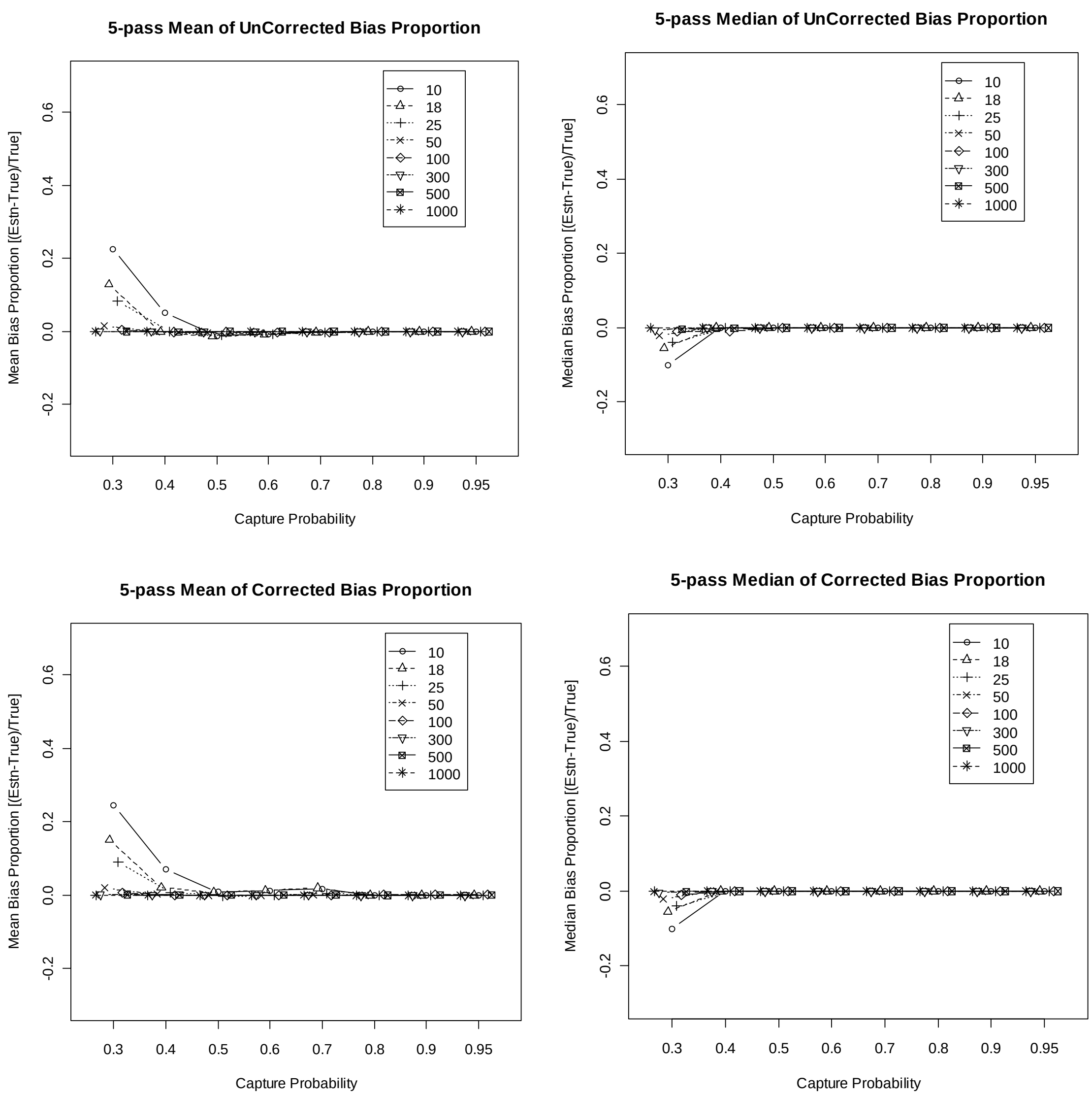


Figure B.4. Comparison of mean (left column) versus median (right column) proportional population estimate bias ([Estimate-True]/True) for five-removal uncorrected (top row) and bias-corrected (bottom row) population estimates by true capture probability (x-axis) and population size (different lines).

APPENDIX C

ROOT MEAN SQUARE ERROR (ROOT-MSE)/ESTIMATED BIOMASS

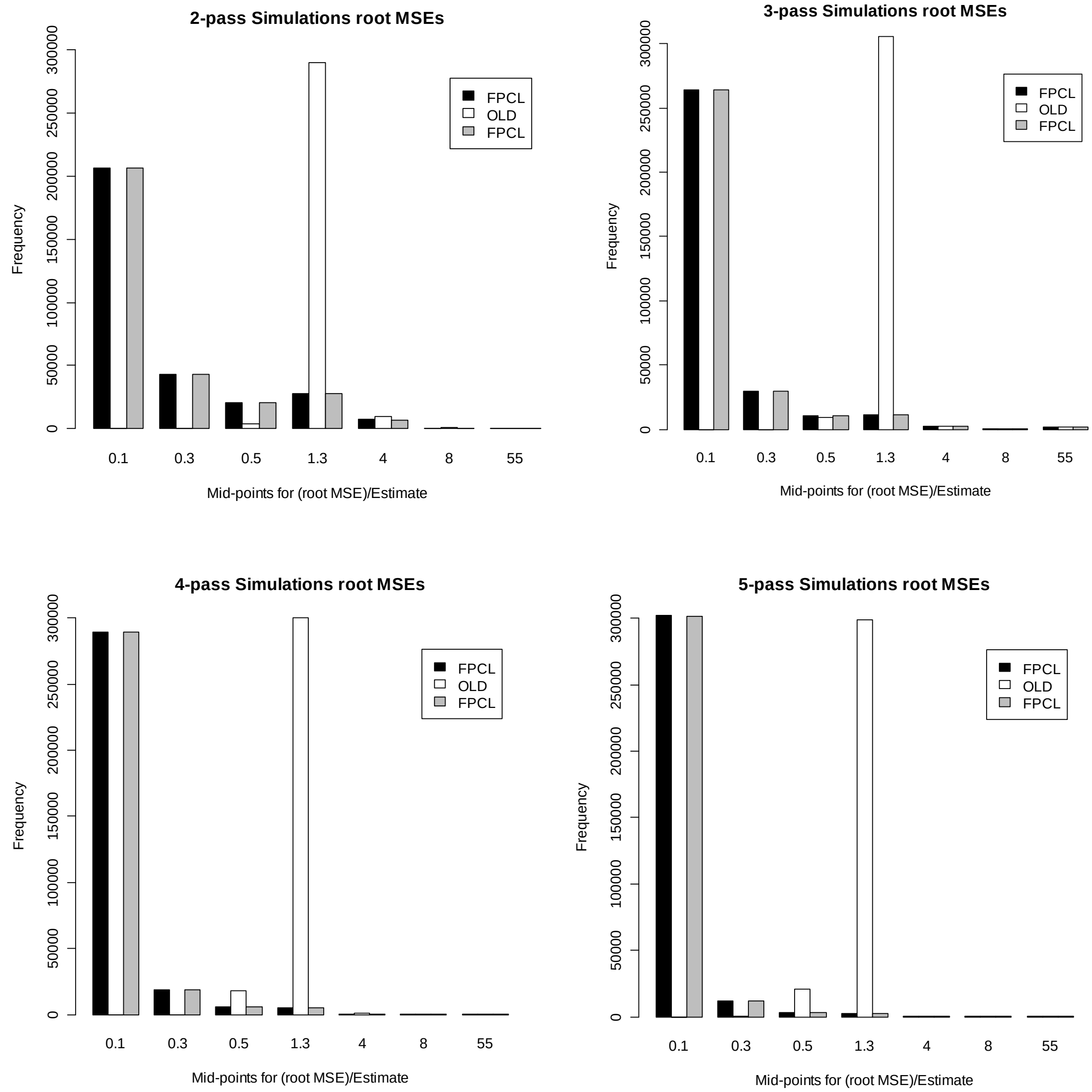


Figure D.1. Distributions of root-MSEs for biomass estimates divided by estimated biomass for simulations of two- through five-removal estimates. Mid-points of bins are show along the x-axes and these bins are not uniform above 0.5.

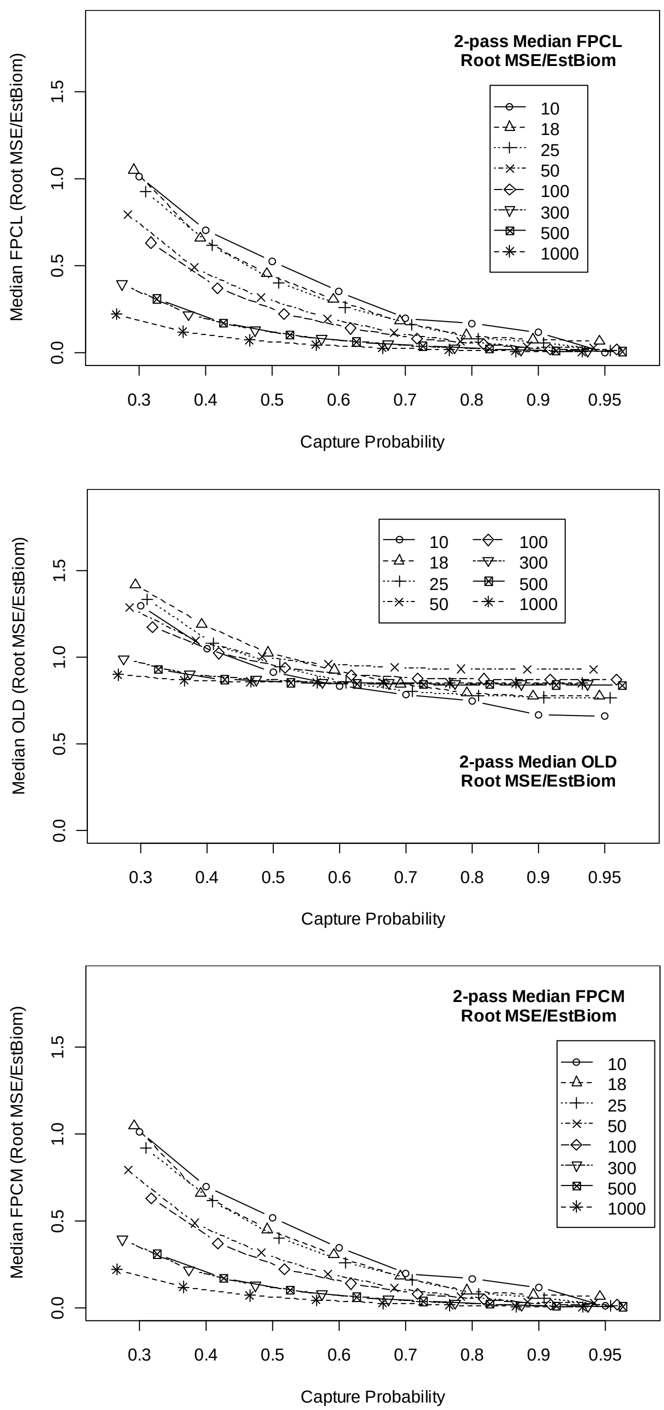


Figure D.2. Median root-MSE divided by estimated biomass for two-removal estimates of biomass by true capture probability (x-axis) and true population size (lines) for the FPCL, OLD, and FPCM and methods (top to bottom graphs, respectively).

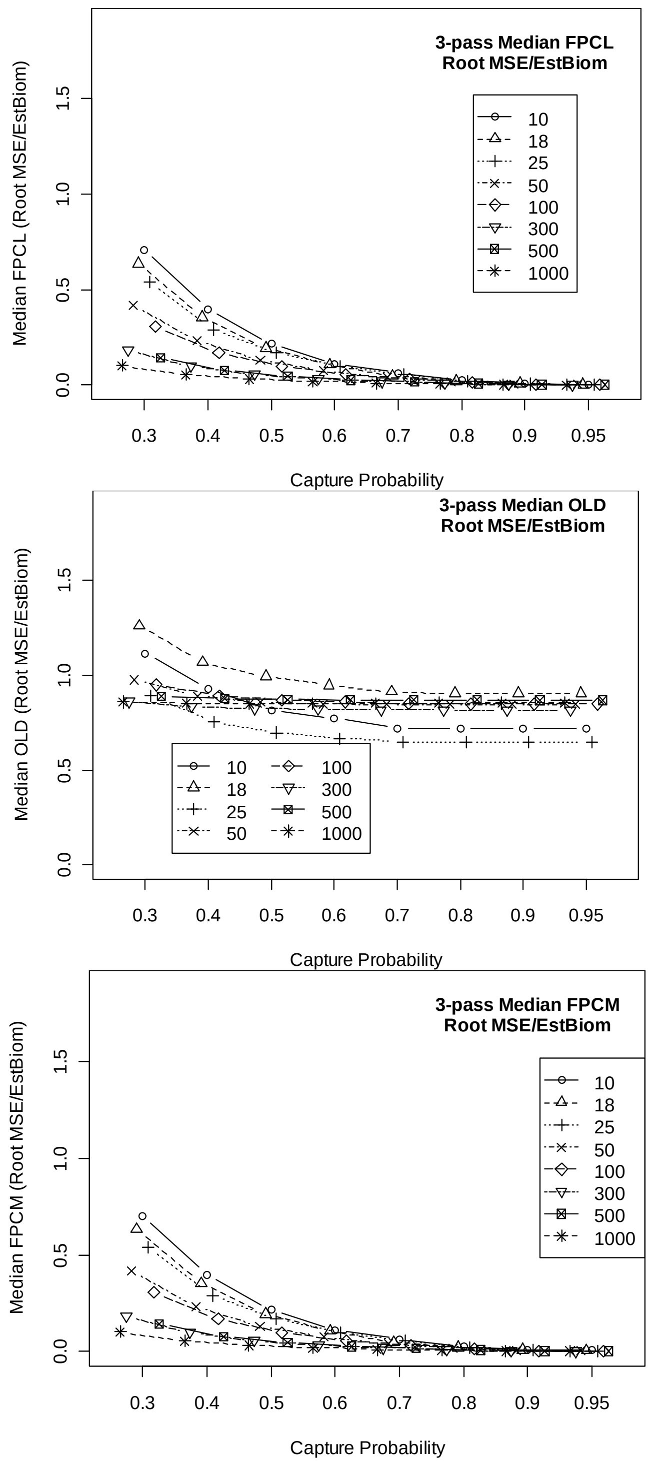


Figure D.3. Median root-MSE divided by estimated biomass for three-removal estimates of biomass by true capture probability (x-axis) and true population size (lines) for the FPCL, OLD, and FPCM and methods (top to bottom graphs, respectively).

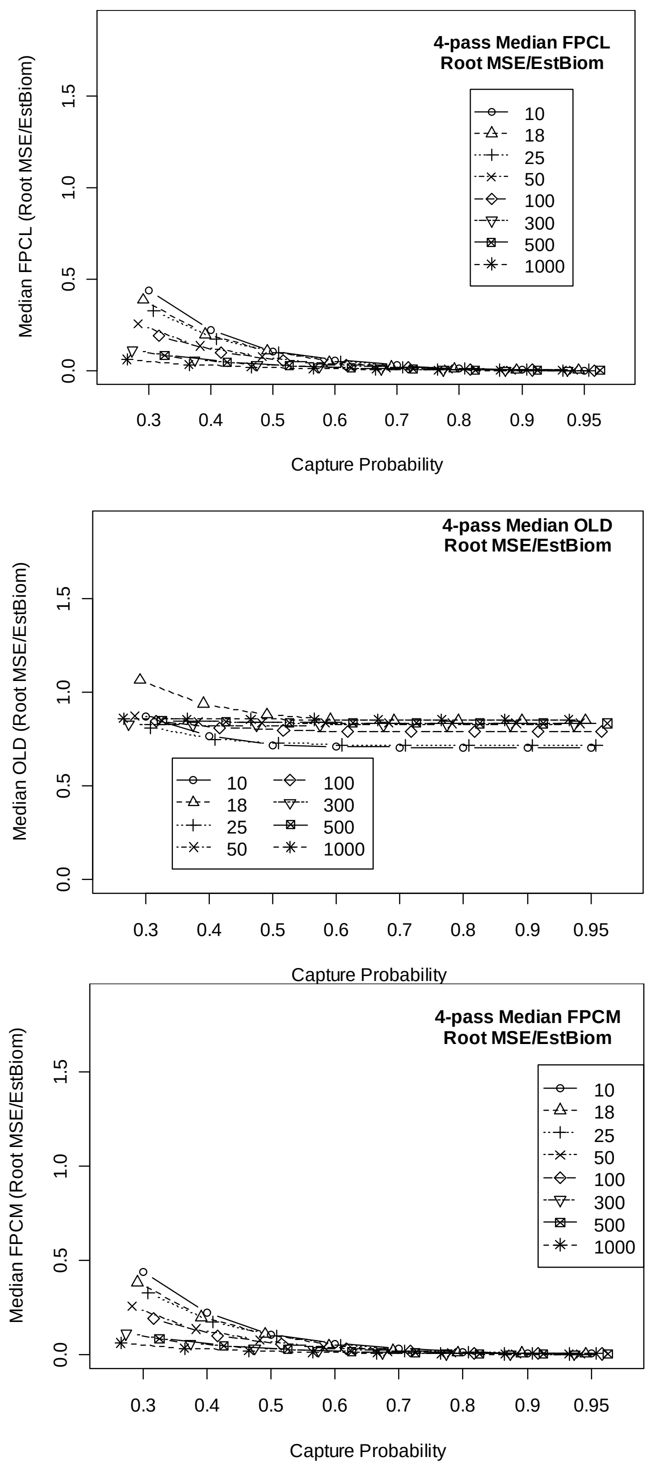


Figure D.3. Median root-MSE divided by estimated biomass for four-removal estimates of biomass by true capture probability (x-axis) and true population size (lines) for the FPCL, OLD, and FPCM and methods (top to bottom graphs, respectively).

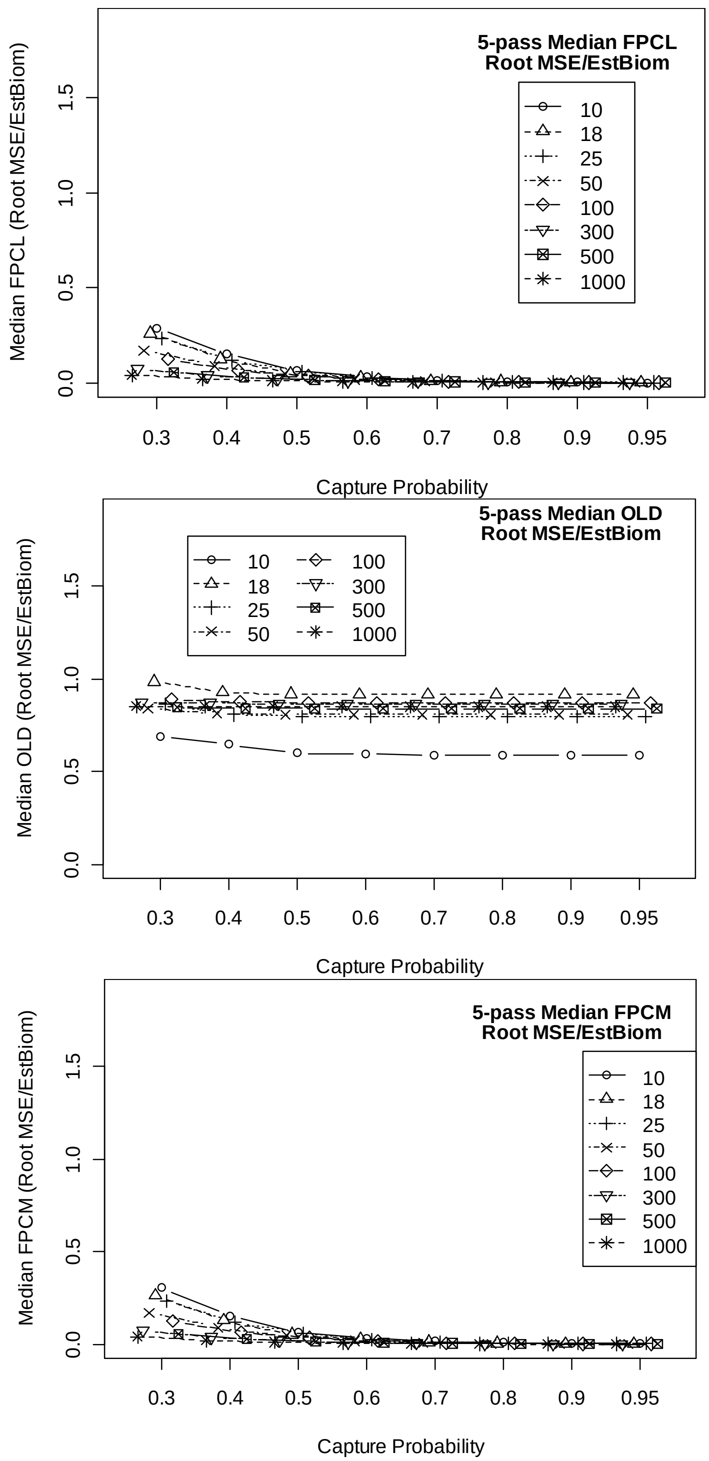


Figure D.4. Median root-MSE divided by estimated biomass for five-removal estimates of biomass by true capture probability (x-axis) and true population size (lines) for the FPCL, OLD, and FPCM and methods (top to bottom graphs, respectively).

APPENDIX D

BIOMASS ESTIMATES FOR CUTTHROAT RESPONSE STUDY

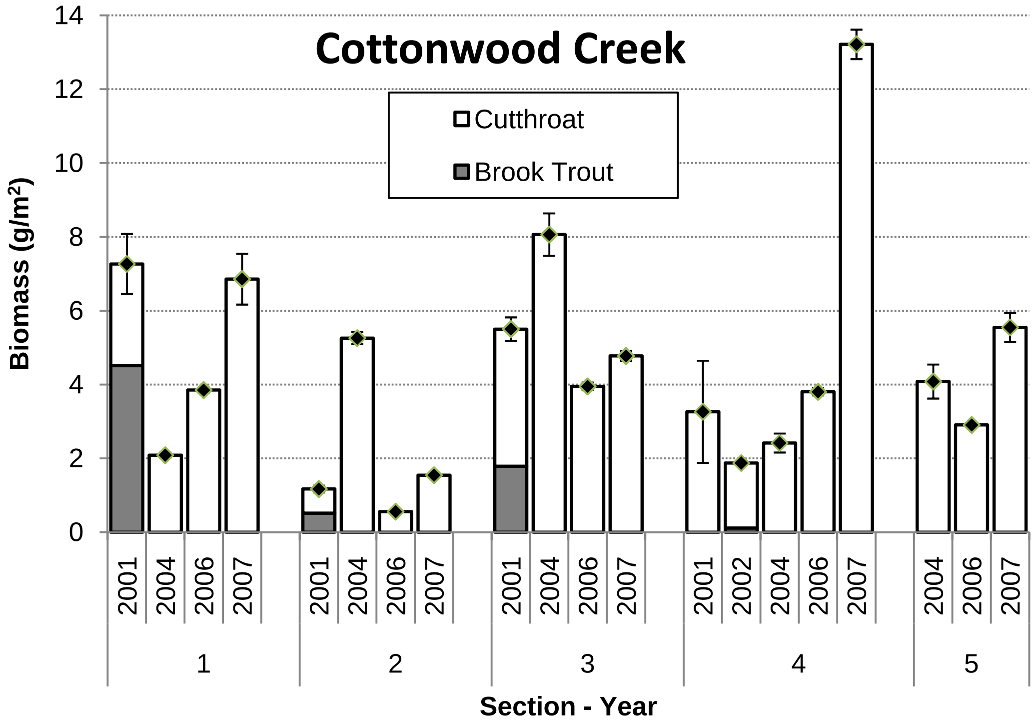


Figure F.1. Biomass estimates for brook trout (gray bars) and westslope cutthroat trout (white bars) by section and year in Cottonwood Creek. Filled circles are total estimates and 95% CIs are shown as capped lines around filled circles. Only years with estimates are shown on x-axis.

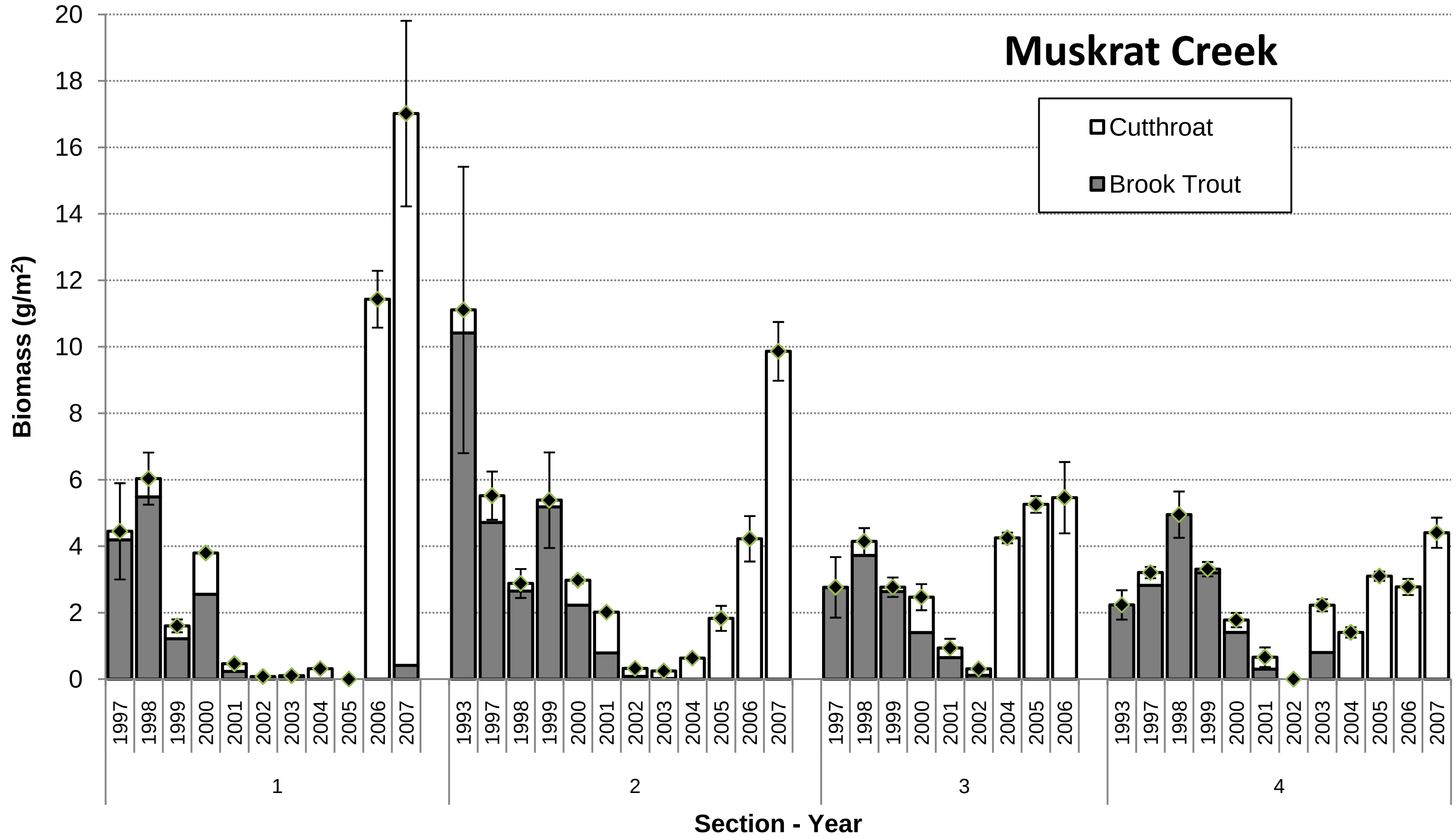


Figure F.2. Biomass estimates for brook trout (gray bars) and westslope cutthroat trout (white bars) by section and year in Muskrat Creek. Filled circles are total estimates and 95% CIs are shown as capped lines around filled circles. Only years with estimates are shown on x-axis.

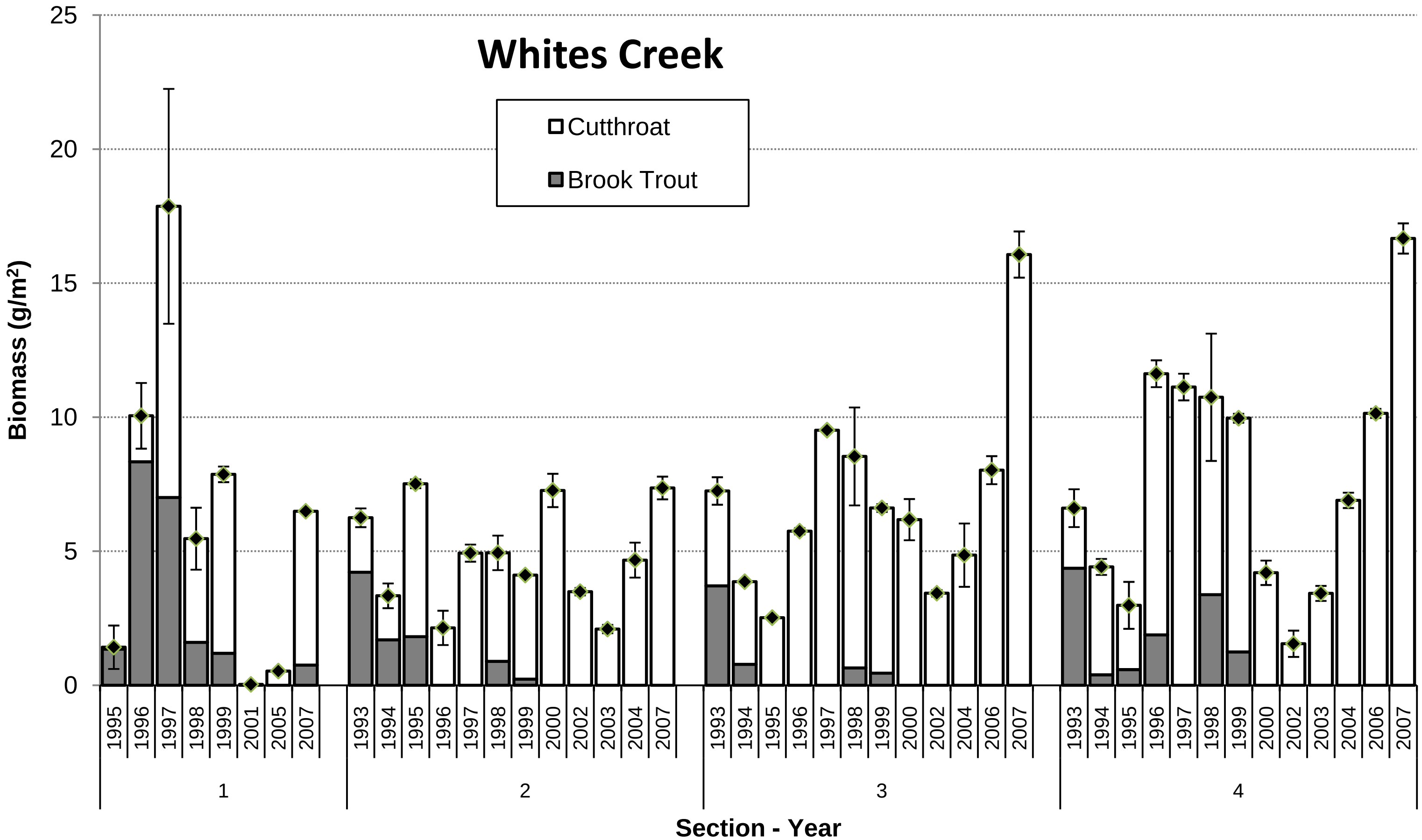


Figure F.2. Biomass estimates for brook trout (gray bars) and westslope cutthroat trout (white bars) by section and year in Muskrat Creek. Filled circles are total estimates and 95% CIs are shown as capped lines around filled circles. Only years with estimates are shown on x-axis.