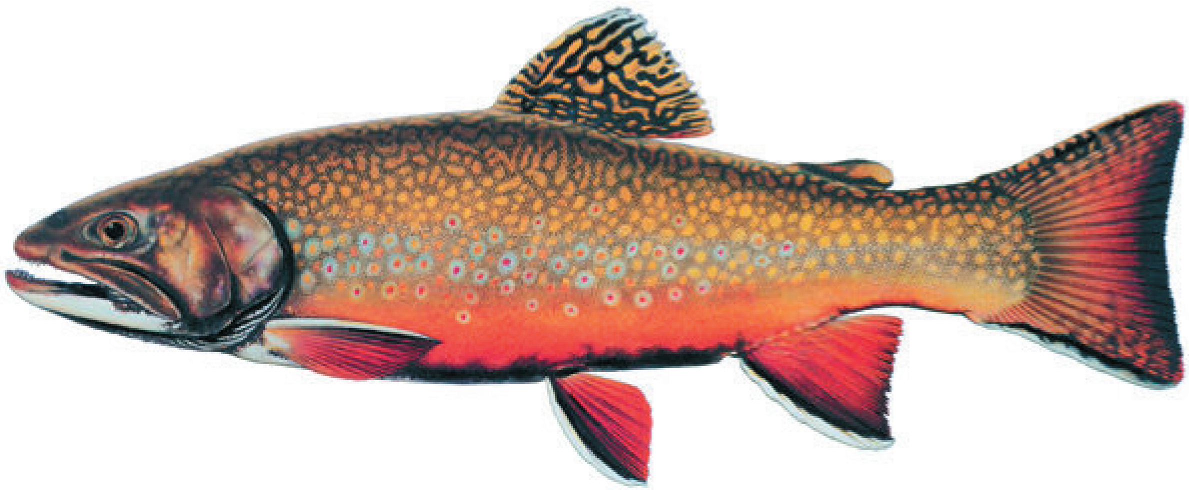
Brook Trout (*Salvelinus fontinalis*): A Technical Conservation Assessment



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Acknowledgments

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Authors' Biographies

Ashley Ficke received her MS in Fisheries from Colorado State University in 2006. Her research studied the effects of low-head diversions on small plains fishes of the Colorado Front Range. Currently, she is working for GEI Consultants, Inc. as a fisheries ecologist and pursuing her PhD at Colorado State University.

Douglas Peterson received his PhD in Fisheries from Colorado State University in 2002. His research interests include trout invasions and the population ecology of inland cutthroat trout.

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Cover Illustration Credit

Summary of Key Components for Conservation of Brook Trout

Brook trout (*Salvelinus fontinalis*) are native to much of northeastern North America, south through the Appalachian Mountains, and west to the Mississippi River headwaters. Intentionally introduced into western North America beginning in the mid 19th century, brook trout are now among the most common salmonids in small stream habitats. In the Rocky Mountain Region (Region 2) of the USDA Forest Service, self-sustaining nonnative brook trout populations are found in Colorado, Nebraska, South Dakota, and Wyoming, but they are most widespread and abundant in mountain streams and lakes in Colorado and Wyoming. Brook trout are a game fish in Region 2, but fisheries for larger nonnative brown trout (*Salmo trutta*) and nonnative rainbow trout (*Oncorhynchus mykiss*) are generally perceived as having greater socioeconomic value. Brook trout are often considered a nuisance species, especially in Colorado and Wyoming, where they have displaced and often continue to threaten populations of native inland cutthroat trout (*O. clarkii*). At the time of this assessment, data that would permit a regional-scale assessment of trends in distribution and abundance of brook trout were not readily available.

Brook trout in Region 2 exhibit considerable plasticity in life history expression. Two ends of this continuum are populations that are fast-growing, mature in their second year, and rarely live past age 4 or 5 versus populations that are slower-growing, mature in their fourth or fifth year, and can live 10 years or more. Population growth rates of brook trout are sensitive to changes in annual survival for young-of-the-year and age-1 stages, and also survival from egg to age-0. Land- and water-management activities that affect these life stages (e.g., through dewatering, altered flow regimes, siltation, and decreased water quality) can affect population age-structure, abundance, and biomass of wild brook trout populations. Habitat fragmentation that limits movement of larger fish within and among streams is also expected to reduce the resilience of local populations.

Distinct longitudinal distribution patterns are frequently apparent in stream networks where nonnative brook trout co-occur with native and other introduced salmonids in Region 2. Brook trout (and native cutthroat trout) are typically found in small, higher-gradient cold temperature headwater streams whereas nonnative brown trout and rainbow trout occur further downstream in larger, warmer waters. Despite these patterns, displacement of brook trout by brown trout has been documented both in Region 2 and in the native range of brook trout. Displacement of brook trout by rainbow trout has also been documented and is major conservation concern for brook trout populations in the southern portion of their native range. Increases in water temperature associated with various climate change scenarios may result in an upstream shift (i.e., to higher elevations) in the downstream distribution limit of brook trout, as warmer water temperatures facilitate upstream encroachment of and displacement by brown trout and rainbow trout. Especially in Colorado and Wyoming, resource managers will likely continue to target brook trout populations for removal or suppression where their presence threatens the existence of native greenback (*Oncorhynchus clarkii stomais*), Colorado River (*O. c. pleuriticus*), and Rio Grande cutthroat trout (*O. c. virginalis*).

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INTRODUCTION

Goals

This conservation assessment of brook trout (*Salvelinus fontinalis*) was performed for the Species Conservation Project for the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS) (http://www.fs.fed.us/r2/projects/scp/assessments/index.shtml) (**Figure 1**). An assessment on brook trout was included as part of the Species Conservation Project because the brook trout is a Management Indicator Species (MIS) on several national forests in Region 2, they are valued as a recreational fishery in some locations, and their invasions have led to displacement of native inland cutthroat trout (*Oncorhynchus clarkii*).

The primary focus of the assessment is on the biology and ecology of brook trout, which is meant to synthesize the current state of knowledge throughout Region 2 in order to improve our understanding of land management's potential effects and to facilitate various management decisions. The assessment is also intended to provide pertinent information regarding brook trout management to aid USFS planning and management activities. The brook trout is a nonnative game species that is actively managed in some locations, so a brief summary of the present management of brook trout by management agencies within states encompassed by Region 2 is also included in the assessment. The scope and specificity of the information provided in the assessment is necessarily limited by the large geographic region encompassed by Region 2 and the complex array of fisheries management objectives that arise from brook trout's status as a game species and its history as an introduced species and effects on native cutthroat trout.

Scope, Uncertainty, and Limitations

As a game species that has been introduced throughout North America and the world, the brook trout has been the focus of much research. Information on brook trout ecology and biology was primarily drawn from research conducted outside of Region 2 because much of the basic research on the species

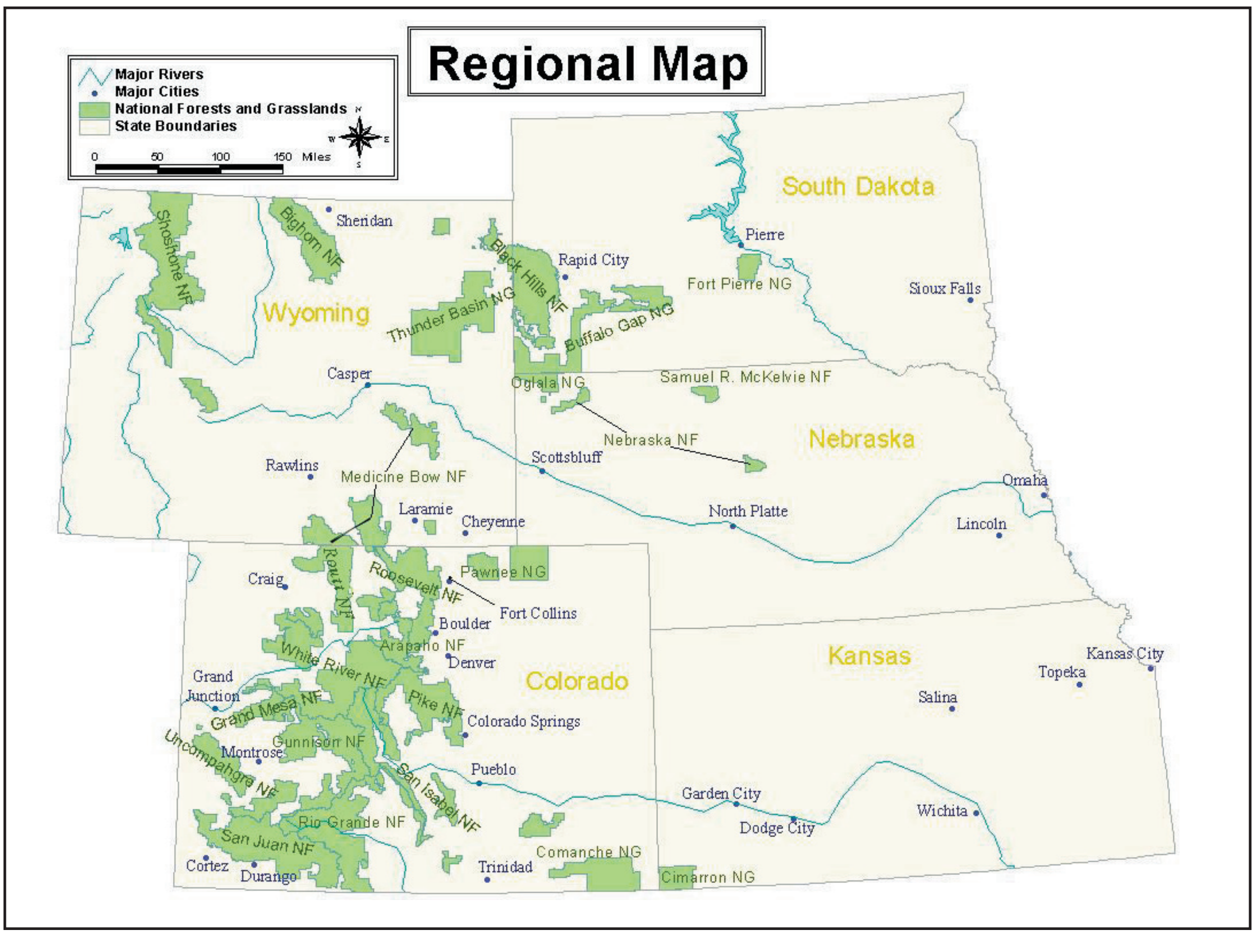

Figure 1. National forests and grasslands within USDA Forest Service, Rocky Mountain Region (Region 2).

comes from populations occurring in its native range in eastern North America. There was less information available to be obtained from studies of populations within Region 2, but these data are emphasized to increase the assessment's applicability to Regional conservation and management issues. The information synthesized in this assessment is primarily drawn from published texts and peer reviewed articles in technical journals. Theses, dissertations, and agency publications provided additional information.

The brook trout is a game species in many waters within Region 2, but it is often considered a nuisance species where they interact with native species like cutthroat trout. Variation in environmental conditions over time and among locations, as well as differences in water, land, and fisheries management, has no doubt affected brook trout populations in Region 2. A comprehensive summary of the range of variation present among populations and management programs in the states encompassed by Region 2 was not feasible for this assessment. Instead, this assessment emphasizes the basic biology and ecology of the brook trout, particularly for populations occurring in Region 2 where such data are available. The synthesis of this information is intended to provide managers with detailed knowledge of the species that can be used as a resource when planning and evaluating various management activities. The assessment also identifies gaps in knowledge of brook trout biology and ecology within Region 2 that may impede effective management and that may be used to guide future research.

To draw conclusions regarding the biology, ecology, and management of the brook trout given the relative paucity of available Region-specific information, we generalize from studies of brook trout conducted outside the Region and also from studies of other stream-dwelling salmonids. Throughout the assessment, we note whether the information presented is derived from studies of brook trout in Region 2, from elsewhere in the species' range, or from studies of other species. Given the diversity of aquatic habitats occupied by brook trout and the variation in life history observed across its range, we caution that while generalizations and conclusions presented in the assessment may be largely valid, they may not be accurate in every case.

Web Publication and Peer Review

This assessment will be published on the USFS Region 2 World Wide Web site (http://www.fs.fed.us/r2/projects/scp/assessments/index.shtml). The peer review of the assessment was facilitated by the American Fisheries Society of America.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status and Existing Regulatory Mechanisms

USDA Forest Service

The brook trout is designated as a Management Indicator Species (MIS) in Region 2, and is used as project- and Forest-level indicators of species viability. As a MIS, the brook trout is used to estimate effects of planning alternatives on fish and wildlife populations (36 CFR 219.9 (a) (1)), and to monitor the effects of management activities on species by evaluating population trends (36 CFR 219.9 (a) (6)). At least six Region 2 forests utilize brook trout as management indicator species: Arapaho-Roosevelt, Medicine Bow-Routt, Pike-San Isabel, Rio Grande, San Juan, and White River, but there is a perception that they may be less sensitive to habitat degradation than other wild trout species (e.g., Shoshone National Forest 2000). For example, a study in South Dakota's Black Hills showed that brook trout were not vulnerable to small to moderate changes in water temperature or turbidity, but they did exhibit detectable responses to changes in stream morphometry (Modde et al. 1986).

Conversely, brook trout are considered a threat to native Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) in Region 2 (Hirsch et al. 2006, Young 2008), and their populations may be reduced by targeted management actions. For example, USFS Regions 2 and 4, the U.S. Bureau of Land Management, the National Park Service, and the U.S. Fish and Wildlife Service (as well as state agencies in Colorado and Wyoming) are among the signatories of a conservation agreement that advocates removal of nonnative fishes as a possible tool to protect cutthroat trout populations (CRCT Conservation Team 2006).

State agencies

Except for Kansas, all states within Region 2 have naturalized, self-sustaining brook trout populations. Brook trout are considered sport fish and are actively harvested. The primary regulatory mechanisms are angling regulations, which vary by state. In all states in Region 2, anglers are required to purchase a fishing license, and some states require trout permits. Limit stocking of brook trout by state agencies still occurs in at least two states within the Region.

Angling regulations

Brook trout are considered part of an aggregate of salmonid species for the purposes of regulation in all four Region 2 states that contain naturalized populations. In Nebraska, brook trout are designated a sport fish, and the daily bag limit and possession limits are seven and 14 fish, respectively (Nebraska Game and Parks Commission 2007). In South Dakota, brook trout are designated a game fish, and the statewide daily and possession limits for trout are five and 10 fish (South Dakota Department of Game, Fish and Parks 2007). One exception is along the border with Nebraska, where the daily and possession limits are each seven fish.

In Colorado and Wyoming, fishing regulations for brook trout are more liberal, perhaps, in part, because brook trout are considered a threat to native cutthroat trout (e.g., Colorado River cutthroat trout). Brook trout may be targeted for eradication in some waters (e.g., CRCT Coordination Team 2006, CRCT Conservation Team 2006, Hirsch et al. 2006). In Colorado, brook trout are designated a game fish, and anglers can possess 10 brook trout (8 inches or less) in addition to the statewide daily bag and possession limits of four and eight fish (Colorado Division of Wildlife 2007). In Wyoming, brook trout are considered a sport fish, and anglers can possess 10 brook trout (8 inches or less) in addition to the general trout possession limit of six fish (Wyoming Game and Fish Department 2007). Additional regulations apply to specific waters throughout the state and primarily consist of differences from statewide bag and possession limits, minimum length limits, tackle restriction, and seasonal or annual closures of some waters to fishing (see Wyoming Game and Fish Department 2007). Tackle restrictions exist on some waters to protect native cutthroat trout.

Stocking

Past stocking has greatly expanded the distribution of brook trout outside their native range (MacCrimmon and Campbell 1969, Fuller et al. 1999). Stocking continues in some waters in Region 2, but current management practices generally aim to prevent further range expansion. Although rainbow trout and brown trout are generally considered the primary target species in salmonid fisheries in the region, brook trout are still stocked in Colorado and Wyoming in order to increase recreational angling opportunities. In Wyoming, stocking is primarily limited to reservoirs and ponds, and the state stocks approximately 40 sites annually (Wyoming Game and Fish Department, unpublished data). In Colorado, brook trout are planted in habitats where native fishes are absent and where fish communities downstream are not likely to be affected (K. Kehmeier personal communication 2007). Brook trout are not cultured in South Dakota, but wild fish are sometimes transferred between drainages to meet angling demand (S. Hirtzel personal communication 2007).

Biology and Ecology

Systematics and general species description

Brook trout are in the family Salmonidae and the subfamily Salmoninae. They are technically considered char, or members of the genus *Salvelinus*. This species and the lake trout, *S. namaycush*, appear to be the basal members of the genus from which other species have radiated (Crespi and Fulton 2004). However, the relatedness of other species within the genus is somewhat unclear, presumably due to extensive hybridization (Crespi and Fulton 2004). Within Salmonidae, the genus *Oncorhynchus*, which includes all species of inland cutthroat trout, is the most closely related to *Salvelinus*, and the fishes in these two genera share many life history characteristics (Crespi and Fulton 2004).

Brook trout can hybridize with bull trout (*Salvelinus confluentus*), which are native to the northwestern United States, British Columbia, and Alberta (Kanda et al. 2002), but they typically do not naturally hybridize with other salmonid species found in Region 2. In hatcheries, however, brook trout have been crossed with brown trout (*Salmo trutta*) to produce tiger trout (*S. fontinalis* × *S. trutta*), or with lake trout to produce splake (*S. fontinalis* × *S. namaycush*). The hybrids are believed to be sterile and have been stocked within Region 2 to create or supplement recreational fisheries (e.g., Satterfield and Koupal 1995). Tiger trout are present in Colorado and Wyoming (Fuller 2007a), and splake have been collected in Colorado, Wyoming, and South Dakota (U.S. Geological Survey 2007).

There are apparently two phylogenetically distinct races of brook trout within their native range in eastern North America: a southern strain, native to waters in the southern Appalachian Mountains, and a northern strain more widely distributed across the northeastern United States and Canada (Stoneking et al. 1981, McCracken et al. 1993, Hayes et al. 1996, Danzmann et al. 1998, Habera and Moore 2005). The northern race is typically characterized by greater heterozygosity and lower diversity of mitrochondrial and nuclear DNA, consistent with larger population sizes or persistent gene flow among populations (Guffey et al. 1999, as cited in Habera and Moore 2005). Southern brook trout are not only genetically distinct from northern populations, but they also exhibit significant among-population genetic heterogeneity consistent with population isolation or small effective population sizes.

Naturalized brook trout populations in Region 2 presumably trace their ancestry to the northern strain. However, this conclusion is tentative and based primarily on historical accounts of hatchery culture and stocking. The southern strain of brook trout was difficult to raise in hatcheries (Lennon 1967), whereas the northern strain was extensively cultured in hatcheries and even stocked to replenish depleted populations of southern brook trout (Sherrill et al. 2001). MacCrimmon and Campbell (1969) report that brook trout were transported to the western United States from New York by train in 1872; so we infer that these fish are derived from the northern strain of brook trout (Wiltzius 1985). A phylogenetic analysis of brook trout that includes samples both the native and introduced ranges may help to confirm the presumed ancestry of brook trout in Region 2.

Adult brook trout in stream habitats in Region 2 are easily identified relative to other salmonid species. Their dorsal surface ranges in color from dark green (olive) to black, and this dark coloration is interrupted by pale yellow, wavy markings called vermiculations, which also extend onto the dorsal fin (Page and Burr 1991, Behnke 2002). The caudal fin is blunt or only slightly forked, and the pelvic and anal fins are typically dark orange with black pigment behind a white leading edge. Sexually mature males are often dark orange and black on their ventral surface. Distinguishing lateral coloration includes light yellow spots, and dark pink or red spots with blue rings (halos).

Distribution and abundance

Brook trout are native to much of eastern North America: their range extends northward to the Atlantic drainages of Newfoundland, Labrador, and Quebec, westward to Minnesota and Wisconsin, and southward to northern Georgia (Behnke 2002). Brook trout have been extensively introduced to fresh waters of the American West since the late 19th century (MacCrimmon and Campbell 1969, Wiltzius 1985), and they have been reportedly introduced to 35 states (Fuller et al. 1999). The brook trout is one of the most widely distributed nonnative fishes in western United States streams and is often the most abundant species where it occurs (Behnke 2002, Schade and Bonar 2005).

Regional scale

Despite the widespread occurrence of naturalized brook trout populations in the western United States (Rahel 2000, Schade and Bonar 2005), we found for this assessment that it was not possible to assess regional (Region 2) trends in the distribution and abundance of brook trout. Data on brook trout distribution and abundance reside with various management agencies and research institutions in the Region. However, the need to compile these data, assess their reliability, standardize abundance or biomass estimates based on different sampling methods, and analyze the dataset quickly put a quantitative evaluation beyond the scope of this assessment. Even when reliable data are available, natural variability in abundance of trout can also complicate assessment of population trends (Platts and Nelson 1988). Thus, our regional-scale assessment of brook trout population status and trends is cursory.

Brook trout appear to be widely distributed in mountain areas of Region 2, especially in the Rocky Mountains (**Figure 2**). They are present in the Arkansas, Colorado, North Platte and South Platte river systems in Colorado. In Wyoming, they are present in the Colorado (Little Snake, Green River, and Great Divide basins), Bear River, Belle Fourche, Yellowstone, Wind-Big Horn, Tongue, Powder, Cheyenne, North Platte, and South Platte river systems (Baxter and Stone 1995). Brook trout are less widely distributed in South Dakota, where they are restricted primarily to the Black Hills in the southwestern corner of the state (Fuller 2007b, South Dakota GAP Analysis Project, http://wfs.sdstate.edu/sdgap/fish/brook%20trout.htm). In Nebraska, brook trout occur in a number of small streams in the Basin, Niobrara, North Platte, Republican, and White/Hat river basins (S. Schainost personal communication 2007). Historical records document the past occurrence of brook trout in Kansas (**Figure 2**; Fuller 2007b), but they do not appear among the list of fish species considered in the state's aquatic GAP analysis program (http://www.k-state.edu/ksaquaticgap/products.html).

Generally, the fishery biologists from Region 2 with whom we spoke considered the brook trout populations to be stable. For example, brook trout were considered the most common salmonid in the Arapaho-Roosevelt National Forest in central Colorado (K. Sexton personal communication 2007); and their range appears to be stable or increasing in the Medicine Bow-

Routt National Forest in Wyoming (G. Eaglin personal communication 2007).

Management agency surveys designed specifically to detect population trends in brook trout are generally rare from Region 2 or are collected concurrent with surveys targeting other fish species. Management and conservation of native greenback (*Oncorhynchus clarkii stomais*), Colorado River, and Rio Grande cutthroat trout (*O. c. virginalis*) are primary fishery resource concerns in Region 2 forests (U.S. Fish and Wildlife Service 1998, Alves et al. 2004, Hirsch et al. 2006), and data on occurrence and density of brook trout are often collected concurrent with, or secondary to, monitoring and restoration activities for cutthroat trout.

An additional source of information on the occurrence of brook trout in Colorado and Wyoming may be available within the next one to two years. The Forest and Rangeland Ecosystem Science Center of the U.S. Geological Survey (USGS), Rocky Mountain Research Station of the USFS, Colorado State University, and collaborators within state agencies have assembled a large dataset on the occurrence of both native and introduced salmonid species in the western United States (J. Dunham personal communication 2007). The dataset will be used to relate fish distributions to environmental variables (e.g., stream size, water temperature, stream discharge, landscape morphology) derived from a geographic information system (GIS), and should identify large-scale patterns in occurrence of brook trout relative to gradients in these variables. The dataset (hereafter USGS-RMRS-CSU dataset) is not currently available but should eventually be posted on a USFS (e.g., http://www.fs.fed.us/rm/boise/index.shtml) or USGS Web site (e.g., fresc.usgs.gov/).

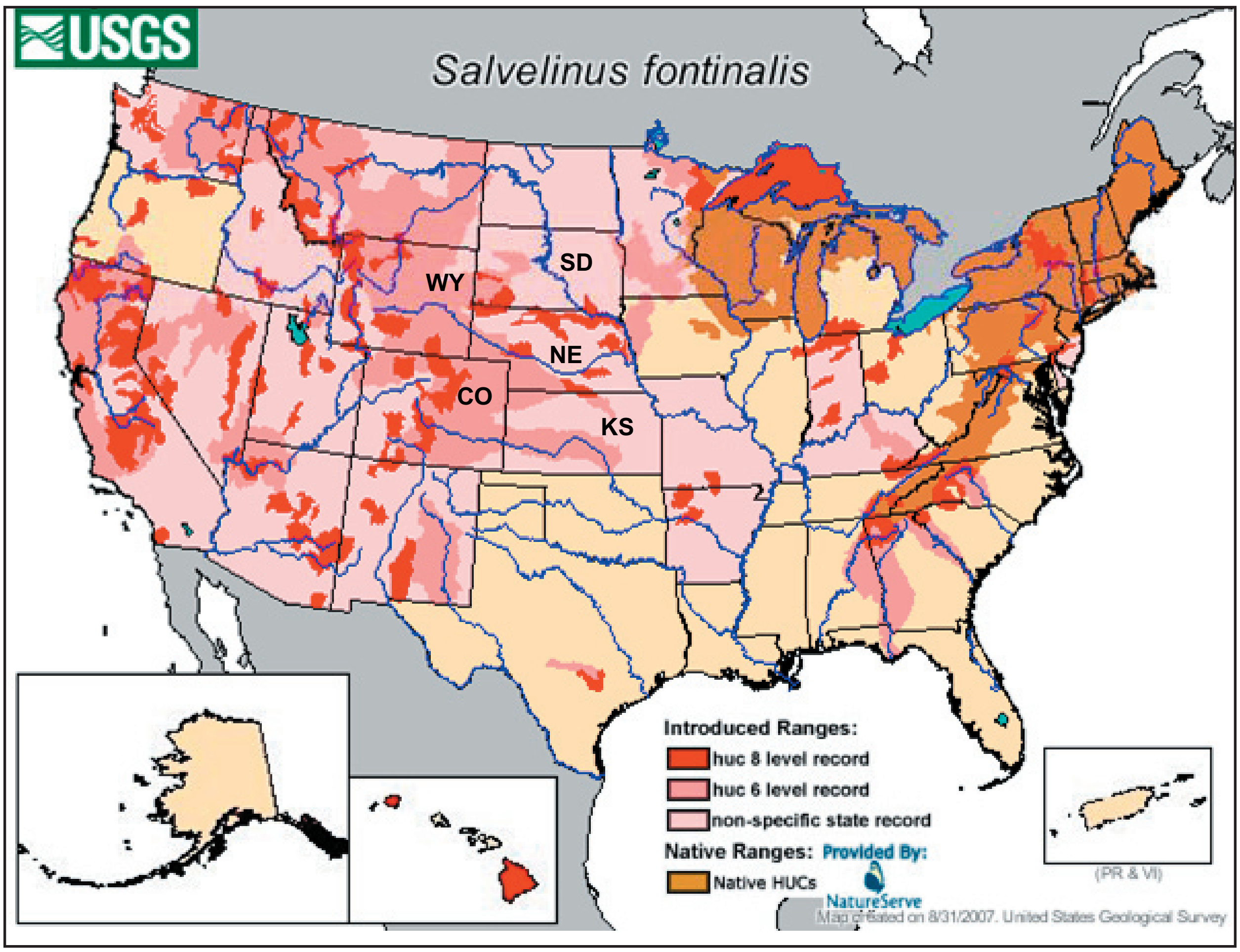

Figure 2. Occurrence of brook trout in the continental United States (http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=939). The distribution is based on previously-documented occurrence within a specific hydrologic unit, or occurrence within state boundaries (i.e., non-specific).

Local scale

Relatively few studies have rigorously investigated the population ecology of brook trout in specific streams within Region 2, but the data from these studies are consistent with a species that can exhibit considerable temporal and spatial variation in abundance. Local mortality, reproduction, emigration, and immigration can drive these fluctuations. The combination of high variation in abundance and the possible effect of immigration and emigration complicate both the detection of trends in abundance and attributing those trends to any specific environmental or habitat-related factor.

Robust time series data on brook trout populations in Region 2 streams are limited. Two studies that intensively studied brook trout populations in the region over four or more years demonstrated that fluctuation is common and of large magnitude, especially for younger age classes. First, Riley and Fausch (1992) and Gowan and Fausch (1996a) used three-pass electrofishing and weirs to evaluate the effect of habitat improvement (installation of log-drop structures) on fish populations of six Colorado streams over eight years. They found that abundance and biomass of adult fish, primarily brook trout, brown trout, and rainbow trout, increased in treatment reaches (log-drop structures) relative to controls (no-log drop structures). They attributed much of the increase to immigration from outside the study area, rather than increased local reproduction. In the control reaches of the five streams where brook trout were common, the density of juvenile (age-1) brook trout fluctuated 3- to 5-fold, and the density of adult brook trout fluctuated 2- to 3-fold across the five streams during eight years. Within a given stream, adult density was generally greater than juvenile density.

Second, Peterson et al. (2004) conducted a removal experiment using two-pass electrofishing and mark-recapture to study the effects of brook trout on Colorado River cutthroat trout in four Colorado streams over four years. Brook trout abundance was manipulated in two streams (treatments), but not in two others (controls). In the mid-elevation control stream (East Fork Parachute Creek, elevation ~2540 m), the density of age-0 brook trout varied 4-fold (121-537 per 250 m), and the density of age-1 and age-2 and older brook trout varied at least 2-fold (age-1: 67-127 per 250 m, age-2 and older: 72-188 per 250 m). In contrast, the density of age-2 and older brook trout in the colder, higher-elevation control stream (Indiana Creek, elevation ~3190 m) was less variable (~8-14 per 250 m) over the four years (Peterson et al. 2004). Given spatial and temporal variation in brook trout abundance and the potential influence of emigration and immigration (Riley et al. 1992, Gowan et al. 1994, Gowan and Fausch 1996b, Peterson and Fausch 2003a), rigorous experimental or monitoring designs may be needed to detect population trends and to suggest causation.

Models to predict occurrence and abundance

A number of studies have related trout abundance or biomass to habitat variables in Region 2 or developed models to predict abundance or biomass of salmonids (e.g., Scarnecchia and Bergersen 1987, Kozel and Hubert 1989a, Hubert et al. 1996), including brook trout (e.g., Chisholm and Hubert 1986, Kozel and Hubert 1989b). For example, Kozel and Hubert (1989b) found that the abundance of brook trout in 32 stream reaches in the Medicine Bow National Forest, Wyoming, decreased as stream size increased; they attributed this to decreasing habitat quality (for brook trout) and interactions with brown trout at lower elevations. Kozel and Hubert (1989a) found that brook trout standing stock was positively correlated to bank cover, and negatively related to drainage density, average reach width, and width-to-depth ratio. However, the predictive ability of these models is uncertain. Fausch et al. (1988) reviewed models to predict standing crop of stream fish and identified a number of data and statistical issues that can limit their utility.

In western U.S. waters outside of Region 2, a few studies have related the occurrence or production of small brook trout to reach- or landscape-scale habitat features. In Montana, Adams (1999) found that brook trout reproduction was often localized at specific locations within a stream reach (e.g., near beaver ponds) and referred to these areas as “nodes” of production. In Idaho, Benjamin et al. (2007) examined factors associated with the occurrence of brook trout in Panther Creek, a tributary to the Salmon River. They found a strong association between occurrence of small brook trout (<150-mm fork length [FL]) and the proximity of unconstrained valley bottoms, which apparently correlate with suitable spawning habitat for char (e.g., Baxter et al. 1999) or presence of source and refuge habitats such as beaver ponds.

Habitat Suitability Indices (HSI) have been developed for a number of salmonid species, including brook trout (Raleigh 1982). These models attempt to assess habitat suitability by reviewing species habitat preferences and requirements (e.g., in terms of temperature, depth, dissolved oxygen), and then transforming these relationships into a scaled, mathematical relationship. Raleigh (1982) cautions that the HSI models for brook trout should be treated as species-habitat hypotheses, not causal relationships. It should be noted that much of the supporting literature for the brook trout HSI comes from the species' native range outside of Region 2.

The few models that have been developed to predict brook trout occurrence in mountain streams within Region 2 generally focus on specific geographic areas. For example, Bozek and Hubert (1992) used survey data from 91 stream reaches in the Colorado and Missouri river basins in Wyoming, and discriminant analysis to classify whether brook trout would be present based on elevation, gradient, and wetted width. Their model accurately predicted the presence (86.9 percent correct classification) or absence (56.7 percent correct classification) of brook trout, which were generally classified as a high elevation, high-gradient, narrow-stream species based on the sign of model coefficients.

Empirically-derived relationships between occurrence or abundance and habitat or environmental characteristics have been developed for other salmonid species in the region, and they may provide analytical approaches useful for comparable models for brook trout. For example, Rahel and Nibbelink (1999) modeled occurrence of brown trout in the North Platte River drainage in Wyoming as a function of stream size and mean July air temperatures ranging from 19 to 22 °C, and concurrent analyses indicated that brook trout tended to occur in small streams (<4 m wetted width) where average July air temperature was approximately 19 °C. They suggested that accounting for land use, basin geology, and geomorphology might improve the predictive ability of the model. Harig and Fausch (2002) developed a logistic regression model to predict the likelihood of establishing Rio Grande and greenback cutthroat trout populations based on habitat characteristics, and they found that cold water temperature <7.8 °C inn July, lack of deep pools, and narrow stream width limited translocation success. In addition, Coleman and Fausch (2007b) found that streams with 800 to 900 degree days will permit recruitment in some years, while streams with 900 to 1200 degree days are best candidates for translocation efforts. Streams with less than 800 degree days appear to be not suitable for translocation (Coleman and Fausch 2007b). Brook trout can displace cutthroat trout from these marginal habitats (e.g., Harig et al. 2000) and the two species may occupy similar niches, so the Harig and Fausch (2002) model may provide some general guidance on the expected occurrence of brook trout in unsurveyed streams. Peterson et al. (2008) present a Bayesian belief to analyze tradeoffs between invasion threat (by brook trout) and the threat of isolation for westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). A component of their model estimates the probability that brook trout will successfully invade stream habitats in the northern Rocky Mountains based on a review of literature and expert opinion.

Additional empirical data would assist in developing more powerful predictive models. The analyses of the aforementioned USGS-RMRS-CSU dataset, or a similar dataset, may provide the basis for such a model.

Behavior and activity patterns

Regional-scale factors, such as geology and climate, interact with local factors such as disturbance regime to create a patchy mosaic of habitats in stream environments that can be both spatially and temporally variable (Schlosser and Angermeier 1995, Fausch et al. 2002). Consequently, the spawning and rearing, foraging, and refuge habitats necessary for stream fishes to complete their life histories may be both discrete in time and space. Movement and ranging behavior can help fish like brook trout to facilitate their ecological needs in a variable environment (**Figure 3**; Schlosser and Angermeier 1995). The evidence that brook trout can be quite mobile even in small streams within Region 2 (e.g, Riley et al. 1992, Gowan et al. 1994, Gowan and Fausch 1996b, Peterson and Fausch 2003a) indicates that movement (e.g., migration, dispersal, ranging behavior) between metapopulations can play a key role in their population ecology. Thus, movement will be a recurrent theme in subsequent discussions of behavior and activity patterns. We caution, however, that the variation in movement behavior of brook trout and other stream fishes resists simple categorization (e.g., Rodríguez 2002, Schrank and Rahel 2004). Even within a single population of stream fishes (e.g., bluehead chub [*Nocomis leptocephalis*] and creek chub [*Semotilus atromaculatus*]), some individuals may be comparatively sedentary while others may move long distances (Skalski and Gilliam 2000).

Spawning

Brook trout spawn in the fall (Hazzard 1932, Power 1980 and references therein), and presumably exhibit some degree of site-fidelity characteristic of salmonids (e.g., Quinn 1993). In Region 2, brook trout exhibit a tendency to move upstream in both summer (Gowan and Fausch 1996b, 2002) and fall (Peterson and

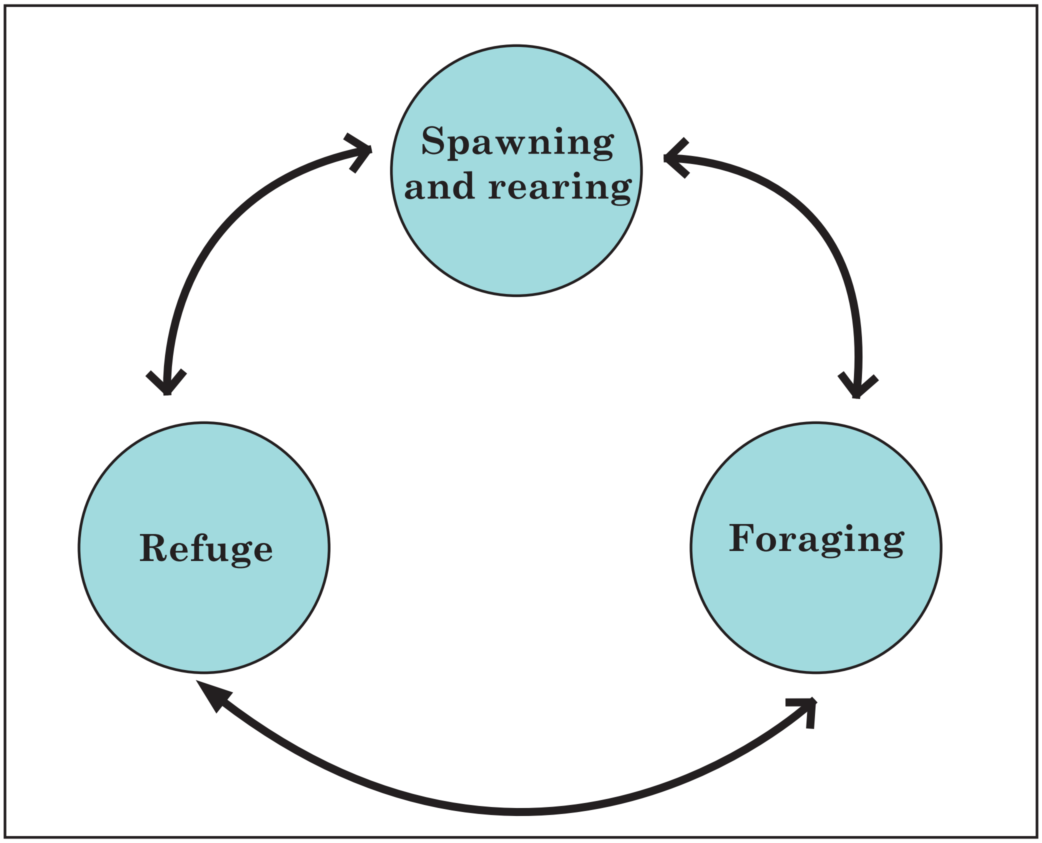

Figure 3. Conceptual diagram showing how movement (arrows) can link necessary fish habitats (circles) when such habitats are discontinuous in space and time (after Schlosser and Angermeier 1995).

Fausch 2003a). Movement in the fall likely represents migration (homing) to natal habitat or ranging behavior to seek suitable spawning habitat. Water temperature appears to be pivotal in determining the timing of spawning activity of brook trout, at least in their native range (e.g., Baril and Magnan 2002). Natal homing in brook trout has been studied in eastern North America, and results are consistent with some degree of site fidelity (e.g., Baril and Magnan 2002, Bernier-Bourgault and Magnan 2002) and demonstrate that brook trout can move tens of kilometers to return to spawning locations (e.g., a sea-run population in New Brunswick, Canada, Curry et al. 2002). Hutchings and Gerber (2002) studied sex-based dispersal and movement patterns during the spawning period in an unexploited brook trout population in Newfoundland, Canada. They found that males moved more frequently and dispersed longer distances than females did, presumably to reduce the likelihood of kin competition (for access to females), decrease the likelihood of spawning with a related female, and increase chance for successful spawning including multiple spawning opportunities.

Homing to natal habitat is presumed to occur at larger scales (10^2-10^3 m), and evidence for site fidelity on a microhabitat scale (1-10 m) is more equivocal. Data from Quebec and Ontario indicate that some brook trout return annually to the same lake inlet (Bernier-Bourgault and Magnan 2002) or location within a lake (Ridgway and Blanchfield 1998); further study revealed that about a quarter of the mapped redd sites were used in multiple years (25 percent, Essington et al. 1998; 23 percent, Ridgway and Blanchfield 1998).

Natal homing in brook trout has not been studied in Region 2. Thus it is not known if the frequency and spatial scale of homing (and conversely straying) differs between the native and introduced ranges of brook trout and whether any differences, if present, contribute to the apparent success of brook trout in western North America.

The physical characteristics of brook trout spawning habitat are discussed in a following section (see **Habitat**).

Rearing and feeding

As juvenile stream fishes grow, their habitat requirements and diets often change (ontogenetic shifts). Typically, energetic needs and the size of feeding territories increase (Keeley 1998, Keeley 2001), which can lead to a decrease in local population density, a mechanism referred to as self-thinning (e.g., Dunham and Vinyard 1997). Although there is strong evidence that territory size drives self-thinning in many salmonid populations (Atlantic salmon [*Salmo salar*], Grant and Kramer 1990; steelhead [Keeley 2001], evidence for self-thinning in brook trout is equivocal. For example, Dunham and Vinyard (1997) analyzed long-term (5 to 9 years) survival data from four streams in the western United States and found no evidence of self-thinning in brook trout. In fact, territoriality may break down, and brook trout may school under certain situations (Schroeter 1998, Dunham et al. 2002). Generally, however, after switching from maternal to exogenous feeding sources after emergence, foraging brook trout generally defend feeding territories. The post-emergent period when juveniles exist at high density may be a critical period for these fish requiring specific habitats and resources (e.g. low-velocity areas in pools or at stream margins, small prey; Armstrong and Nislow 2006). McFadden (1961) studied the population dynamics of a brook trout population in Lawrence Creek, Wisconsin during 1953-1957 and found that a high density of young brook trout was associated with lower survival. Density-dependent effects in survival of young brook trout have also been documented in Region 2. For example, the survival of juvenile brook trout decreased with increasing density of juvenile conspecifics in a Colorado stream (Peterson et al. 2004), and survival was inversely related to the density of adult salmonids in six Colorado streams (Latterell et al. 1998).

Density-dependent emigration from postemergent habitats may be a key behavior used by small fishes to locate appropriate habitat and resources. This behavior has been documented in brown trout and Atlantic salmon (Armstrong and Nislow 2006, Einum et al. 2006). However, it appears that juvenile fish do not move far. For example, a study of brook trout in a West Virginia stream found that juvenile density was correlated with the density of spawners in the previous fall and remained seasonally constant (Petty et al. 2005). The ability to move in search of resources is probably limited by swimming ability, which is length-dependent (Northcote 1997). On the other hand, lake-spawned brook trout from Meach Lake, Ontario emigrated into streams shortly after emergence, possibly to avoid high temperatures in the littoral zone of the lake (Curry et al. 1997). Movement of newly emerged brook trout probably varies locally and depends upon factors such as the density, availability of food and habitat, predation risk, and stochastic events like storms that would increase stream discharge and water velocity and lead to physical displacement of smaller individuals.

Adult brook trout exhibit ranging behaviors to locate resources that are variable in space and time (Schlosser and Angermeier 1995, Fausch et al. 2002, Gowan and Fausch 2002, Petty et al. 2005). Compared to juveniles, their greater swimming ability allows them to move greater distances and presumably to exploit a wider range of habitats. In Region 2, Gowan and Fausch (2002) studied the foraging-related movement of brook trout in a Colorado stream. They concluded that brook trout exhibit reach-scale (10^2 m) ranging behavior to locate optimal feeding positions, which allows them to maximize energy intake in a temporally variable environment (Gowan and Fausch 2002).

Refuge

Refuge habitats are important to help fishes escape harsh seasonal abiotic conditions (e.g., high water temperature, low water temperature, ice scouring, high flows) and disturbance. Refuge habitats can consist of reach-scale characteristics such as deep pools and groundwater inputs and structure such as large woody debris (LWD) and debris dams. In winter, trout in Rocky Mountain streams often seek deep pools that are less likely to freeze to the bottom and that also provide a refuge from ice scour (Jakober et al. 1998, Harig and Fausch 2002, Lindstrom and Hubert 2004). In their native range, brook trout become more gregarious in winter, and they are more frequently found in pools beneath overhead cover and in proximity to sources of groundwater discharge (Cunjak and Power 1986). Groundwater is thought to help maintain high-quality winter refuge for fishes by providing ice-free habitat (Power et al. 1999, Brown et al. 2006). The importance of groundwater increases with latitude, and fish may migrate long distances to select winter habitat with aquifer discharge (Power et al. 1999). On the other hand, radio-tagged cutthroat trout and brook trout in Cottonwood Creek, Wyoming, avoided reaches downstream of groundwater inputs because of unstable ice formations such as frazil and anchor ice (Lindstrom and Hubert 2004). In addition, structures such as cobble, boulders, LWD, and undercut banks provide important winter habitat for both adult and juvenile brook trout in the western United States (Meyer and Gregory 2000).

Pools and groundwater discharge are also important elements of refuge habitats during summer months. For example, groundwater discharge approximates regional mean annual temperature and can buffer high summer water temperatures (Meisner et al. 1988). During summer months, salmonid fishes may not be uniformly distributed and may instead seek specific patches having suitable thermal characteristics (e.g., Torgersen et al. 1999).

Habitat

Brook trout require specific habitats at certain stages of their life history. Though the required habitats for spawning, rearing, foraging, and winter refuge are not necessarily mutually exclusive, they are often spatially separated or variable in time (Fausch et al. 2002). Some populations of brook trout, like other salmonids, can be highly mobile animals, moving extensively to fulfill their life history.

Thermal characteristics

Basic physiological requirements tend to confine brook trout in Region 2 to cool or coldwater streams, lakes, and beaver ponds that have high levels of dissolved oxygen. Brook trout are coldwater fish, with an optimum temperature range of 10 to 14 °C (Power 1980). Similarly, McMahon et al. (2007) found that that peak growth of age-0 brook trout in allopatric laboratory trials was 14.0 °C, but in allopatry with bull trout the optimum shifted upwards to 15.6 °C. The ability of brook trout to tolerate higher temperatures appears to be somewhat unusual among char. For example, Selong et al. (2001) placed Arctic char (*Salvelinus alpinus*) and bull trout in a coldwater group of salmonids based on their critical thermal maximum (CTM), whereas brook trout were placed in higher-CTM group along with rainbow trout and brown trout. In general, rainbow trout and brown trout are believed to have higher optimum temperature ranges (up to 22 °C) than brook trout (Peterson et al. 1979, Behnke 2002). High water temperatures (22 to 24 °C) can physiologically stress brook trout (Taniguchi et al. 1998, Rahel and Nibbelink 1999), and brook trout tend to avoid water greater than 24 °C (Raleigh 1982). Attempts to acclimate brook trout to 26 °C resulted in 100 percent mortality (Taniguchi et al. 1998).

Low water temperatures may limit the distribution of brook trout, especially at high elevations, by preventing recruitment of juvenile fish. Shuter and Post (1990) proposed a general mechanism for this observation in temperate aquatic ecosystems, whereby low water temperatures prevent juveniles from growing enough in their first summer to survive the winter without starving (e.g., Cunjak and Power 1987). Empirical data from the western United States tend to support the hypothesis that very cold summer water temperatures (<7.8 °C) may limit brook trout distribution (and other salmonids; Harig and Fausch 2002, Coleman and Fausch 2007).

In Region 2, Peterson et al. (2004) generally found greater densities of age-0 and age-1 brook trout in two streams having mean July water temperatures of at least 12 °C, compared with two streams where the mean July temperature was <7 °C. Cluster analysis of fish assemblages in Salt River basin (Wyoming and Idaho) placed brook trout in a group characteristic of high-gradient, high-elevation streams, which was associated with colder water temperatures (Quist et al. 2004). Also in Wyoming, Mullner and Hubert (2005) developed a model to predict maximum July water temperature in headwater streams and reported that the lowest predicted temperature where brook trout were present was 9 °C.

Outside Region 2, Benjamin et al. (2007) reported that the maximum summer stream temperatures ranged from 8 to 19 °C, but brook trout were only present in water that was 11 °C or warmer. Adams (1999) studied fecundity, growth, and age at sexual maturity of brook trout in two Montana streams. Although the two streams (Twelvemile and Moore creeks) exhibited different longitudinal temperature profiles because one had a shallow headwater lake (Moore Creek), Adams (1999) found significant variation in brook trout population characteristics both within and among streams related to temperature. In Twelvemile Creek, age-0 fish became less abundant with increasing elevation (i.e., decreasing stream temperature), and age-2 fish in upstream reaches were smaller than age-1 fish from lower reaches. In Moore Creek, growth and presence of age-0 fish decreased with increasing distance from the headwater lake, which had a warming effect on adjacent stream reaches. Adams (1999) hypothesized that lower individual growth rates (and therefore low fecundity) were limiting population growth, thereby preventing successful colonization further upstream in Twelvemile Creek or downstream in Moore Creek. Few studies have explored the effects of low temperatures (<8.0 °C or <800 degree days) on Region 2 brook trout demographics, but electrofishing surveys of a highmountain stream revealed missing age classes of brook trout, which suggested limited recruitment (Peterson et al. 2004, Coleman and Fausch 2007b).

Temperature can also affect the strength and outcome of interspecific interactions. Condition-specific competition, where the competitive ability of a species depends upon factors such as temperature (Dunson and

Travis 1991), has been documented for a number of salmonid species including dolly varden (*Salvelinus malma*) and white-spotted char (*S. leucomanis*) (Taniguchi and Nakano 2000); brook trout and brown trout (Taniguchi et al. 1998); and brook trout and cutthroat trout (DeStaso and Rahel 1994). Brook trout were competitively inferior to brown trout at very high water temperatures (≥ 22 °C; Taniguchi et al. 1998). In the Horse Creek drainage, Wyoming, brook trout were never sympatric with brown trout when the midday summer water temperature was below 15 °C, but sympatry could occur between 15 and 23 °C (Taniguchi et al. 1998). In contrast, brook trout tend to outcompete native cutthroat trout at higher water temperatures. For example, laboratory experiment with size-matched juvenile cutthroat and brook trout showed that brook trout were competitively equal to cutthroat trout at 10 °C and superior at 20 °C (De Staso and Rahel 1994).

Dissolved oxygen

Brook trout, like other salmonids, require dissolved oxygen concentrations greater than 5 mg/L (Avault 1996), and concentrations of 7 mg/L or more are optimal (Raleigh 1982).

Hydrologic regime

Flow regime appears to be a key factor influencing the establishment and abundance of nonnative salmonids like brook trout (Strange et al. 1993; Fausch et al. 2001), primarily because the timing and magnitude of floods relative to the timing of spawning and emergence can dramatically affect age-class strength (Latterell et al. 1998; Fausch et al. 2001). A number of studies conducted within Region 2 suggest that stream discharge during emergence and early development are the most important because high flows can limit critical juvenile habitat (Anderson and Nehring 1985) or displace newly emerged fish (Latterell et al. 1998). Flow regimes in Region 2 differ from those in the eastern United States in that the spring snowmelt peak within Region 2 is much more pronounced (Fausch et al. 2001), though this more generally applies to Rocky Mountain streams in Colorado and Wyoming. While brook trout have successfully invaded western streams that have different hydrologic regimes that their native systems, the evidence that discharge can affect brook trout recruitment (e.g., Latterell et al. 1998) and the observation that brook trout have yet to invade all accessible waters (e.g., Fausch 1989, Adams et al. 2002) leads to the hypothesis that hydrologic conditions may limit brook trout invasions in certain instances (Dunham et al. 2002, Fausch et al. 2006). Although this has not been directly measured, spring snowmelt floods that mobilize the streambed could destroy alevins and sac fry in the interstitial spaces (Fausch et al. 2006), or they could displace or injure emerging fry (Nehring and Anderson 1993). Juvenile brook trout in Wyoming are often displaced and forced downstream into beaver ponds, where they attain very high densities (Baxter and Stone 1995). This may also be why studies of summertime brook trout movement in Region 2 have found more adults traveling upstream than downstream; this directed movement could be explained in part by displaced individuals moving back upstream. A study of six Colorado streams found that the abundance of age-1 brook trout declined when spring flows increased in magnitude and duration, probably because these flows displaced juveniles or limited their habitat (Latterell et al. 1998).

Channel gradient

Stream channel gradient appears to be an important correlate for brook trout habitat. Brook trout can move through higher-gradient stream reaches, but they are often more abundant in lower- to moderate gradient stream reaches within higher-elevation mountain streams. For example, streams in the Snowy Range, Wyoming with a gradient of at least 7 percent had roughly half the biomass of lower-gradient streams, indicating that brook trout abundance is negatively correlated with stream gradient (Chisholm and Hubert 1986). Fausch (1989) reported that brown trout were less abundant in sympatry with brook trout when stream gradient was greater than 7 percent. An inverse relationship between trout abundance and gradient is not always consistently observed. For example, a study of 18 Wyoming streams showed that sites with moderate (1.8 to 4.3 percent) and high (4.0 to 7.2 percent) gradients contained higher densities of trout than those with lower (0.2 to 1.8 percent) gradients (Isaak and Hubert 2000).

High-gradient stream reaches may also limit the ability of brook trout to access otherwise suitable habitat. Adams et al. (2000) examined the movement of brook trout in several Idaho streams and found that stream gradients up to 13 percent did not limit upstream-directed dispersal. They concluded that nearly vertical falls, rather than steep slopes per se, were more likely to limit upstream movements.

Elevation

Elevation (or correlates such as temperature, stream size, gradient, and productivity) also appears to be related to the presence and abundance of brook trout. In general, brook trout are more likely to be present and present in greater abundance in higher elevation streams (Kozel and Hubert 1989b, Quist and Hubert 2004) and lakes in Wyoming (Chamberlain and Hubert 1996), perhaps in part because higher-elevation sites may be less disturbed by land use and brown trout are less likely to be present (Kozel and Hubert 1989b). Elevation was also the most important predictor of brook trout presence in a study of 30 streams on the eastern slope of the Canadian Rockies, possibly because temperature decreases with increasing elevation (Paul and Post 2001). Paul and Post (2001) also found that elevation predicted the distribution of bull trout and cutthroat trout with greater accuracy than other habitat variables (e.g., substrate, cover, gradient).

Pools and pool-forming agents

Channel gradient and elevation appear to influence brook trout distribution and abundance at larger spatial scales; the presence of specific habitat units or small-scale habitat characteristics are also important determinants. In small streams, brook trout tend to be more abundant in pools (Boussu 1954, Schroeter 1998, Sotiropoulos et al. 2006). Boussu (1954) found that the presence of brush cover and undercut banks was correlated with a higher density of brook trout in a study on Trout Creek in Gallatin County, Montana.

Regional data indicate that brook trout also benefit from the presence of large wood in stream channels, which creates and maintains pool habitat. Large wood is an important habitat-forming agent in subalpine streams in the northern Rocky Mountains (Richmond and Fausch 1995), and the proportion of pools formed by large wood is less in disturbed streams (Fausch et al. 1995). The addition of log drop structures in Colorado streams resulted in an increase in the abundance and biomass of adult trout, including brook trout, though the mechanism behind this response was immigration (Gowan and Fausch 1996a,b). The link between wood and trout habitat has implications for managed forests in Region 2, especially where past activities such as railroad tie driving have removed pool habitat and large woody debris from many montane streams (Young et al. 1994, as cited in Richmond and Fausch 1995). In the Pacific Northwest, a long-term (1973-1997) study of three logged riparian sites (one reference, site A; one clearcut where existing wood and logging debris were left in the stream, site B; and one clearcut where the stream was "cleaned", site C) showed that leaving woody debris in a stream after logging provided fish habitat and prevented streambank instability. Fish densities coastal of cutthroat trout at site B (woody debris not removed) remained similar to those seen at the reference site (Young et al. 1999).

Lentic habitats

Brook trout also utilize lentic habitats in Region 2, and habitat features in those systems appear to influence population structure. In the Medicine Bow and Laramie Ranges in Wyoming, small beaver ponds with a high morphoedaphic index (MEI, total dissolved solids/mean pond depth) contained larger numbers of smaller fish than larger ponds (Winkle and Hubert 1990). Chamberlain and Hubert (1996) reported that small lakes with a high MEI contained larger numbers of smaller fish, whereas larger less productive lakes contained small numbers of large individuals.

Similarly, Johnson et al. (1992) reported on the habitat features and population structure of brook trout in beaver ponds in southeastern Wyoming. They found that some ponds contained primarily large fish (>200 mm total length [TL]) in good condition, whereas ponds contained high densities of small individuals (125-175 mm TL) in poor condition. Proportional stock density (i.e., the ratio of large to small brook trout) was positively correlated to mean pond depth, surface area, volume, and late-summer water temperature, but negatively correlated with the extent of water-level fluctuation and a measure of recruitment potential. Regression analyses found that recruitment potential was the strongest predictor of stock structure, and that beaver ponds having inlet streams (i.e., spawning habitat) tended to support higher densities of smallbodied brook trout (cf., Rabe 1970).

Feeding

Prey type

Brook trout have been described as generalists or opportunistic predators on aquatic and terrestrial insects, crustaceans, mollusks, and sometimes small fish (Power 1980 and references therein; Hubert and Rhodes 1989 and references therein). Although their choice of prey items is often contingent upon availability, prey selection varies among individuals (Allan 1981) and between lentic and lotic habitats (Dynes et al. 1999, Proulx and Magnan 2002). Despite this, there is evidence that brook trout in Region 2 prefer certain invertebrate taxa; for example, individuals not limited by gape size (i.e., adult fish) selected large invertebrates such as Trichoptera (caddisflies) and Plecoptera (stoneflies) in a Wyoming stream (Hubert and Rhodes

1989, Duffield and Nelson 1998). Dunham et al. (2000) studied diets of stream-dwelling brook trout in sympatry with Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) in northeastern Nevada. They found that brook trout consumed primarily insects, including Trichoptera, Diptera (true flies), Coleoptera (beetles), Hymenoptera, and Plecoptera, but they concluded that brook trout were nonselective in their preferences.

Diets of lacustrine (lake-dwelling) brook trout can be more variable and can lead to significant differentiation among individuals selecting prey in a particular habitat. Juveniles and adult brook trout in Canadian Shield lakes often eat zooplankton (Proulx and Magnan 2002). In contrast, a diet study from an alpine lake near Niwot Ridge, Colorado indicated that brook trout ate invertebrates, not zooplankton, and that cannibalism was rare (Toetz 1992). In oligotrophic Canadian Shield lakes with well-separated feeding niches, morphological, genetic (Dynes et al. 1999), and physiological (Proulx and Magnan 2002) differences (i.e. trophic polymorphisms) have developed between brook trout feeding in the littoral and pelagic zones. We are not aware of any studies that have investigated the existence of trophic polymorphisms within brook trout populations in Region 2.

Prey acquisition and behavior

Stream-dwelling brook trout feed on drifting invertebrates of both aquatic and terrestrial origin, and they will also prey on benthic invertebrates (Power 1980 and references therein; Hubert and Rhodes 1989 and references therein) or opportunistically consume trout eggs (Allan 1981). Allan (1981) studied foraging brook trout in Cement Creek, Colorado, and found that they are visual predators that feed primarily during the day. Foraging activity peaked at dawn and dusk in spring and summer and at midday in late summer and autumn. Presumably, this shift in activity tracked a change in the diel pattern of drift availability (Allan 1981, but see Young et al. 1997). Because trout are visual predators, water turbidity reduces their ability to detect drifting prey (Sweka and Hartman 2001). In contrast, sediment deposition may affect feeding by altering the taxonomic composition of benthic invertebrates (Culp et al. 1986). For example, Suttle et al. (2004) used experimental stream channels to examine the effect of fine sediments on steelhead trout. They observed reduced growth and survival of juvenile steelhead because fine sediment deposition tended to favor burrowing invertebrate taxa that were less vulnerable to predation (Suttle et al. 2004). Management activities that elevate turbidity or introduce high levels of fine sediment into the stream would be expected to decrease the foraging success of visual predators like brook trout.

In montane streams like those in Region 2, food is often limited (Allan 1981, Morgan et al. 1999), and its availability is temporally and spatially variable (Gowan and Fausch 2002, Baxter et al. 2005). Although trout are often characterized as drift feeders, they will also take prey such as stoneflies from the benthos (Grant and Noakes 1987a, Duffield and Nelson 1998) and terrestrial insects from the surface (Hilderbrand and Kershner 2004). As drifting macroinvertebrates become rare in late summer and in autumn, brook trout in the western United States rely more heavily upon terrestrial insects that fall into the stream (61.5 percent of total summer diet, Duffield and Nelson 1998; 36.2 percent of total diet in September, Hubert and Rhodes 1989). This reliance on terrestrial or allochthonous input has also been documented for brook trout in their native range (45 to 75 percent of total diet, Webster and Hartman 2005). Allochthonous input varies seasonally and often depends on the characteristics of riparian vegetation. The relative contributions of aquatic and terrestrial insects to Region 2 stream systems are not well quantified. However, it is apparent that dominant vegetation type and riparian health will affect the amount and type of terrestrial input (Wifpli and Musslewhite 2004). For example, Saunders and Fausch (2007) found that livestock grazing regimes can dramatically affect the amount of terrestrial insects available to fish in Wyoming streams.

In addition to opportunistic prey selection, brook trout use a number of feeding strategies or modes. Adult salmonids hold position in a stream and wait for invertebrates that drift downstream, and dominant individuals compete for the most energetically profitable locations (Fausch 1984). However, there is evidence that brook trout select feeding positions on the reach scale (10^2 m), not at the habitat unit scale. For example, Gowan and Fausch (2002) demonstrated that dominant brook trout excluded from their preferred position often exited the pool. They concluded that if feeding positions were selected at the scale of habitat unit, then the most subordinate individuals, not the dominant ones, would have left. Young-of-the-year brook trout will hold position in the current and wait for drifting invertebrates, but they will also actively forage for prey on the surface or the benthos (Grant and Noakes 1987a, McLaughlin et al. 1994).

Fish age or size also affects feeding behaviors. Because an individual's position in a dominance hierarchy depends largely upon its size, older fish tend to occupy the preferred positions (Fausch 1988).

However, a study in Ontario, Canada found that fish become more cautious about foraging as they grow. Disturbed adults take longer to return to their foraging positions than juveniles do, and reaction distance, or distance at which fish cease foraging and flee from potential predators, is much greater for adults than for juvenile fish (Grant and Noakes 1987b). Because areas that provide concealment from potential predators are not necessarily optimal for foraging, this behavior is probably driven by the tradeoff between predation and starvation risk. Because older (i.e., larger) fish are more resistant to starvation (due to increased body size and lipid reserves) and more attractive to predators than smaller ones, they tend to use more caution when foraging (Grant and Noakes 1987b).

Reproduction

During spawning season, females excavate nests, or redds, in which they deposit their eggs. Females often build more than one redd during spawning (Curry and Noakes 1995, Ridgway and Blanchfield 1998). Fertilized eggs are fanned into the interstices between the substrate and covered with small gravel (Power 1980). Brook trout alevins remain in the interstices in the gravel over the winter and emerge in the spring.

The small size of juvenile salmonids makes them vulnerable to displacement by high flows (Nehring and Anderson 1993, Latterell et al. 1998). However, studies in natural systems and artificial channels indicate that this window of vulnerability is fairly short, and varies among species. In a small Norwegian stream, discharge that exceeded ambient flows by 4-100× failed to displace juvenile brown trout ≥ 67 mm in length (Heggenes 1988). A study using swim-up brown trout fry in artificial channels with velocities varying from 0.05 m/sec to 0.35 m/sec showed that the period of vulnerability was only 5 to 6 days after emergence (Daufresne et al. 2005). Nonetheless, high flows during this period can cause significant reductions in the local density of juvenile salmonids, depending upon the available refuge habitat. Newly emerged brown trout and Atlantic salmon in a large Norwegian river were displaced by increasing flows, and estimated losses of Atlantic salmon (i.e., those displaced downstream) were 5.6 to 11.1 percent of total annual fry mortality (Saltveit et al. 1995). As they grow and their swimming ability improves, fish most likely avoid displacement by taking refuge behind structure such as cobbles or boulders (Heggenes 1988, Heggenes and Traaen 1988, Simpkins and Hubert 2000).

Choice of spawning sites by brook trout may involve habitat selection at multiple scales. At a larger scale ($\geq 10^2$ m), salmonids (e.g., Geist and Dauble 1998), and particularly char (e.g., Baxter and Hauer 2000), select spawning sites within so-called bounded alluvial valley segments characterized by high rates of exchange between streamwater and groundwater. At smaller scales ($\leq$ 10 m), the use of sites with groundwater upwelling has been documented for brook trout spawning in lakes (Ridgway and Blanchfield 1998) and streams (Webster and Eiriksdottir 1976, Essington et al. 1998). Groundwater discharge through redds removes metabolic waste products and delivers dissolved oxygen to embryos (Bjornn and Reiser 1991). It also helps to stabilize thermal regimes during critical developmental periods (i.e., over the winter). Baxter and Hauer (2000) studied bull trout in a Montana drainage and found that areas with high exchange rates between surface water and groundwater had virtually no anchor ice, which kills trout embryos. Although groundwater appears to play an important role in selection of spawning sites, brook trout will also build redds at sites without upwelling groundwater (Bernier-Bourgault and Magnan 2002). Site choice in relation to groundwater flow appears to be variable and dependent upon large-scale geologic factors that influence its availability (Curry and Noakes 1995). In lakes, brook trout either build redds (Ridgway and Blanchfield 1998) or deposit their eggs on submerged talus slopes (Power 1980). The association between upwelling groundwater and spawning site preference in brook trout has been well documented in the species' native range, but few data are available from Region 2.

Substrate preference

Brook trout spawn in gravel that is small enough to move during redd excavation (Witzel and MacCrimmon 1983a), but they tend to avoid fine sediments because these reduce embryo survival and emergence success (Power 1980, Alexander and Hansen 1983). For example, brook trout did not construct redds in fine substrates (<4 mm in diameter) in an artificially enhanced spawning site in an Ontario lake outlet (Bernier-Bourgault and Magnan 2002). The presence of fine sediments can reduce the survival rates of pre-emergent brook trout (Witzel and MacCrimmon 1983b), but behavioral tactics can sometimes mitigate these effects. For example, female brook trout remove fine sediments from stream substrates during redd construction (Young et al. 1989), or they may select spawning sites with groundwater upwelling or high velocity surface water that prevents deposition (Curry and MacNeill 2004). Curry and MacNeill (2004) found that the effects of fine sediment on pre-emergent brook trout varied by developmental stage, and they stressed the importance of monitoring multiple life-history stages and understanding local adaptations when investigating overall population-level effects of sedimentation.

Redd superimposition, whereby later spawners build redds on top of existing ones, has been documented for brook trout in their native range (Curry and Noakes 1995, Essington et al. 1998). This is thought to be a result of limited spawning habitat (Ridgway and Blanchfield 1998). However, there is some evidence that females preferentially select spawning sites with existing redds, and that the redd itself makes a site more attractive to spawners (Essington et al. 1998).

Behavior

Both female and male brook trout exhibit mate choice. Males prefer larger females, which are capable of producing more eggs, and females prefer males that are of equal or greater size, perhaps because the incidence of egg cannibalism is lower when a larger male fertilizes a nest (Blanchfield and Ridgway 1999). Males depart after fertilizing the eggs, and no parental care is provided after the female buries the eggs (Hutchings 1994, Blanchfield and Ridgway 1999). Males compete for access to females positioned over redds (Power 1980), and larger males often have greater success fertilizing eggs. A study in Scott Lake, Ontario, found that female brook trout will delay spawning until a smaller male is driven off by a larger one (Blanchfield and Ridgway 1999).

Demography

Variability in life history and demographic characteristics appears to be common in brook trout, including for those populations within Region 2. Life history plasticity can have strong effects on the population dynamics of brook trout (e.g., Hutchings 1993), and there is considerable evidence for such plasticity in brook trout across environmental gradients in Region 2 (e.g., Kennedy et al. 2003). Consequently, the following discussion highlights the distinguishing characteristics of this plasticity and the effects on population dynamics.

Longevity

Brook trout are generally considered to have the shortest lifespan of all char species (Power 1980). However, significant variation in longevity is apparent in both their native and introduced ranges. Brook trout often do not survive for more than 3 or 4 years in streams within their native range and often do not grow larger than 250 mm (McFadden 1961, McFadden et al. 1967, Flick and Webster 1975, Fausch and White 1981, Whitworth and Strange 1983). In contrast, northern or alpine stocks of brook trout, or some populations associated with larger lakes and rivers, can live up to 8 to 12 years and, in non-anadromous stocks, grow up to 400 mm (Power 1980 and references therein). Similar patterns in brook trout longevity are seen within its introduced range. For example, Adams (1999) studied variation in demographic patterns of brook trout within and between two Montana streams and found that few brook trout lived past age 4 or 5 or grew larger than 200 mm TL. In the northwestern United States, Mullan et al. (1992) reported that brook trout in lower elevation streams lived to about age 4, while those at higher elevations lived to age 9. Reimers (1979) reported a maximum age of 24 years in a stunted brook trout in an unproductive high-elevation lake in California.

Data for Region 2 are consistent with variation in longevity among habitats or across environmental gradients such as temperature and elevation. For example, Kennedy et al. (2003) reported on maturity and longevity of brook trout in two streams that differed in elevation and thermal regime. They found that brook trout in the warmer, mid-elevation stream (~2600 m, mean July water temperature 12.5 °C) only lived to age 4 or 5 and were typically <200 mm FL; those in the colder, high-elevation stream (>3100 m elevation, 7.1 °C) often lived 8 to 10 years, and a few were aged 11 to 14 with maximum size up to about 250 mm. Peterson and Fausch (1998) also found that adult brook trout in colder, higher elevation streams in Colorado attained larger body sizes than those in warmer streams. Brook trout from two high-elevation Wyoming streams were also reported to live up to 9 years (Kozel and Hubert 1987). Brook trout in some high-elevation lakes in Region 2 also appear to be long lived. Toetz et al. (1991) reported that brook trout in an alpine lake (3455 m elevation) along the Front Range of Colorado lived up to 13 years and grew up to 281 mm TL. In contrast, so called stunted populations of brook trout can also occur in some systems within Region 2, often within beaver ponds (e.g., Johnson et al. 1992), that are characterized by small body size and few fish older than age 3 (e.g., Rabe 1970).

Maturity

Brook trout are iteroparous (Vladykov 1956, Power 1980, Blanchfeld and Ridgway 1997). However, they do not necessarily spawn each year after reaching maturity (e.g., Hutchings 1994), perhaps because of tradeoffs between energy allocation for reproduction and for overwinter survival (Hutchings et al. 1999).

Age and size at maturity varies between the sexes, and male brook trout generally reach maturity at least one year before females in a given population (e.g., McFadden 1961, McFadden et al. 1967, Kennedy et al. 2003). In two Michigan streams, male brook trout could even reach maturity at the end of their first year of life (McFadden 1961, McFadden et al. 1967).

Similar to the pattern observed with longevity, maturity schedules for brook trout show distinct differences within and among streams whereby maturity is delayed (or occurs at a larger body size) in colder, less productive habitats. In Region 2, Kennedy et al. (2003) found that most female brook trout in a Colorado stream with a mean July water temperature of 12.5 °C matured at age 2 or 3 (some as early as age 1) when body length was ≥ 120 mm FL. In contrast, they typically matured 2 years later, at body size ≥ 170 mm FL, in another stream with a mean July water temperature of 7.1 °C. Slower growth and later maturity were also observed in female brook trout in colder reaches of a Montana stream (Adams 1999).

Age at sexual maturity is plastic, and individuals do not necessarily spawn annually (Hutchings 1994, Kennedy et al. 2003), perhaps because reproduction reduces overwinter survival of both males and females. For example, in Newfoundland, Canada, Hutchings et al. (1999) estimated overwinter survival for reproductive males, reproductive females, and immature individuals (mean TL 116 mm). Overwinter survival rates for these brook trout were 0.27, 0.36, and 0.58, respectively, suggesting that allocation of energy into reproduction reduces the chances of successful overwintering (Hutchings et al. 1999).

Fecundity

The number of eggs produced by female brook trout is positively related to body size (Power 1980). Regression equations that predict the number of eggs produced by females of a given body size (typically length) have been published for brook trout populations throughout North America (**Figure 4**; Allen 1956, Vladykov 1956, McFadden 1961, McFadden et al. 1967, Tripp et al. 1979, Hutchings 1993, Adams 1999). Variation in fecundity is evident both among populations from different regions (McFadden 1961) and among populations in nearby streams (Hutchings 1993, Adams 1999). In Region 2, data on fecundity of brook trout are limited. Allen (1956) reported on fecundity of brook trout from a beaver pond in Wyoming. However, we were not able to locate any published accounts of brook trout fecundity, or body size-fecundity equations, for streams in Region 2. In western North America, Tripp et al. (1979) and Adams (1999) present fecundity equations based on data from stream-dwelling brook trout populations in Alberta and Montana, respectively.

Based on length-at-maturity and maximum body sizes observed for stream-resident brook trout from Region 2 (e.g, Peterson and Fausch 1998, Kennedy et al. 2003), we would expect the number of eggs per female to range from about 50 to 750 (**Figure 4**). For example, the equation of Tripp et al. (1979) predicts that female brook trout of 125, 175, and 200 mm FL would contain approximately 56, 406, and 581 eggs. Adams (1999) fit fecundity relationships for populations in two streams using both length and weight. Both measures of body size were significantly related to fecundity, but she found that weight was the better predictor. However for comparative purposes, Adams' (1999) two equations predict that female brook trout of 125, 175, and 200 mm FL would contain approximately 65 or 119, 344 or 273, and 483 or 351 eggs (predictions for Twelvemile or Moore creeks, respectively). Predictions from the equations of Tripp et al. (1979) and Adams (1999) are consistent with observations from at least one stream-resident brook trout population in Colorado. For example, the mean observed fecundity of brook trout in Willow Creek, Rocky Mountain National Park, based on a sample of 21 female brook trout of mean length 200.1 mm FL (SD = 2.9, range 163-212 mm) was 449 eggs (SD = 19.1, range 312-581 eggs) (D. Peterson, U.S. Fish and Wildlife Service, unpublished data).

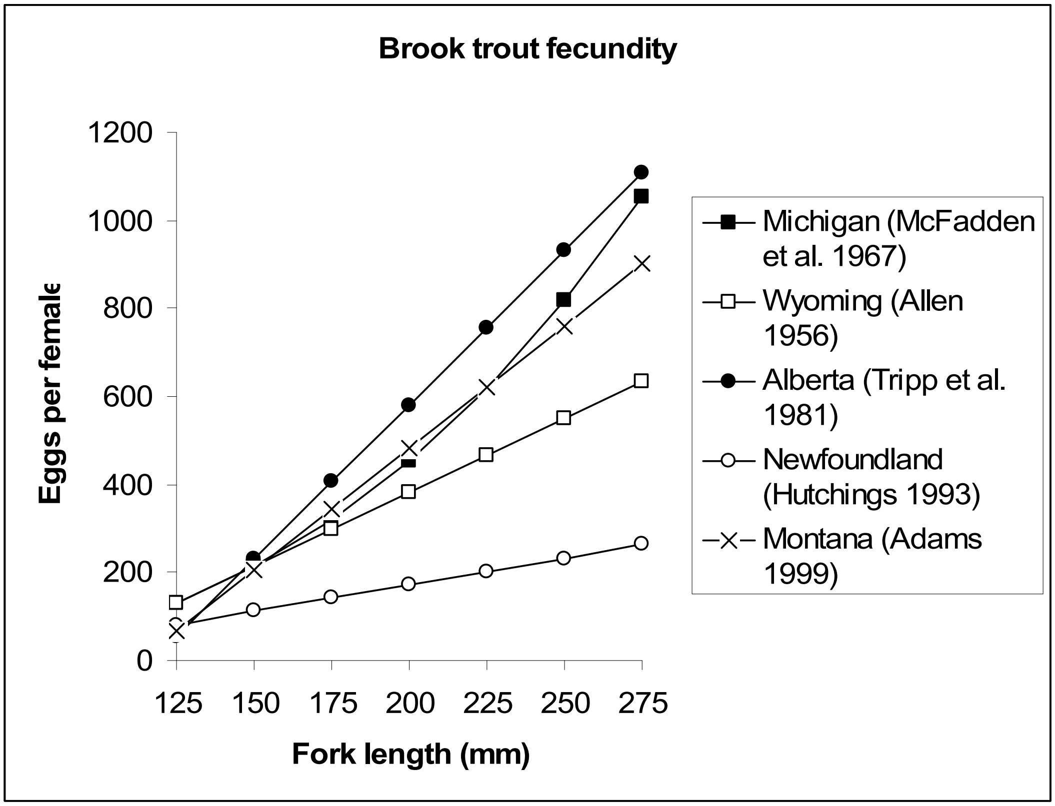

Figure 4. Brook trout fecundity as a function of body length. Plots are a representative example of body size-fecundity regression relationships for brook trout in its native and introduced ranges, standardized to fork length (FL). All populations are from streams except for Allen (1956), which was from a beaver pond. The original regression equations in their original measurement (TL or FL) and units (mm or in) are as follows - MacFadden et al. (1967): log10(eggs) = 0.19248 + (2.69242)(log10(TL, in)); Allen (1956): eggs = -285.7 + 3.34*(FL, mm); Tripp et al. (1979): eggs = 7.0*(FL, mm) - 819; Hutchings (1993) for Freshwater River: eggs = 1.18(length, mm) – 74.26; and Adams (1999) for Twelvemile Creek: eggs = 651.824 + 5.432*(TL, mm).

Survival

Survival (and mortality) of brook trout is influenced by a myriad of abiotic, biotic, and anthropogenic factors. The effect of these factors on the abundance and distribution of brook trout is discussed elsewhere in this assessment. This section will instead focus on variation in empirically-derived survival rates in the context of life history of brook trout as a prelude to a demographic model introduced in a following section.

Survival by life stage varies considerably from egg through adult, and the youngest life stages tend to exhibit the greatest temporal variability. A few studies have provided estimates of stage-specific survival in brook trout based on either long-term time series data on abundance and reproduction (e.g., McFadden 1961, McFadden et al. 1967, Hunt 1969), or mark-recapture methods over multiple years (e.g., Peterson et al. 2004) or between years and seasons (e.g., Carlson and Letcher 2003, Petty et al. 2005).

Perhaps the most comprehensive study of the population ecology of stream-dwelling brook trout is presented in McFadden et al. (1967) who studied an angling-exploited population in Hunt Creek, Michigan over 14 years. They used life table analysis to derive stage-specific survival estimates for 11 different cohorts. They estimated mean egg to age-0 interannual survival (i.e., survival from spawning in fall to age-0 the next fall) as 0.0425 (range 0.02515-0.07905), and found that survival at this stage exhibited greater temporal variation than older stages. Adams (1999) adjusted McFadden et al.'s survival estimates for subsequent age classes to partition natural and fishing mortality, and estimated natural (without fishing) interannual survival rates of 0.4099, 0.3717, and 0.4112 for age-0, age-1 and age-2, respectively.

In Region 2, Peterson et al. (2004) conducted a four-year mark-recapture experiment with trout in four Colorado streams, and estimated interannual survival of brook trout in two of them. In the warmer, mid-elevation stream, stage-specific survival estimates varied through time and appeared to decline as total brook trout density increased. Age-0 brook trout exhibited greater variation in survival (i.e., survival from age-0 in fall to age-1 the next fall, range 0.059-0.483), compared to age-1 (range 0.078-0.479) and age-2 and older (range 0.0564-0.435). Across the duration of the study, they estimated mean apparent survival rates of 0.235, 0.281, and 0.266 for age-0, age-1, and age-2 and older, respectively. In the colder, higher-elevation stream, they estimated apparent survival of 0.563 for age-2 and older brook trout (range 0.374-0.875), but data were not sufficient to provide estimates for younger age classes. Higher adult survival (age-2 and older) in the colder of the two streams is consistent with the prediction from basic ecological theory that high adult survival favors delayed reproduction (e.g., Hutchings 1993).

Seasonal trends in survival have not been studied in brook trout populations in Region 2. Data from other regions suggest that overwinter mortality can be greater than at other times (Carlson and Letcher 2003, Petty et al. 2005).

Movement and population structure

Movement into (immigration) and out of a population (emigration) can have profound effects on the population ecology of all species (Morris and Doak 2002). Because potamodromy is a consistent characteristic of inland salmonid populations (Northcote 1997) and brook trout can also migrate or disperse considerable distances even in small streams (e.g., Gowan and Fausch 1996b, Peterson et al. 2003a), movement patterns both within and among populations can be important determinants of demographic trends at multiple spatial scales.

Within individual populations, movement may link metapopulations from more productive habitats with those in other habitats where vital rates (survival and fecundity) would presumably constrain population growth. For example, Adams (1999) studied the intrapopulation demography of brook trout in two Montana streams and used matrix population models to analyze longitudinal trends in population growth rates. She found that only immigration could explain the persistence of brook trout in some (colder) stream reaches. She also concluded that that the data were consistent with Schlosser and Angermeier's (1995) hybrid source-sink metapopulation model applied at the within-stream scale, whereby in-stream source areas contribute more demographically than sink areas.

Movement may also influence interpopulation demographic variation and persistence of brook trout at larger spatial scales, especially if they exhibit spatial population structure such as a metapopulation. Metapopulation structure is hypothesized to facilitate persistence of a species in an environment characterized by stochastic disturbance events such as fires, floods, and droughts. Metapopulation structure is hypothesized to facilitate persistence of a species in an environment characterized by stochastic disturbance events such as fires, floods, and droughts. Rieman and Dunham (2000) reviewed the evidence for metapopulation structure in stream salmonids. They concluded that spatial structuring and dispersal was evident in many species, but variation in those patterns confounded simple generalizations of metapopulations. Schlosser and Angermeier (1995) proposed five variants of metapopulation models for stream fishes and found evidence for hybrid metapopulation dynamics from two published studies of cyprinids (minnow species) and anadromous salmonids.

At least one study has demonstrated watershed scale population structure in brook trout. For example, Rogers and Curry (2004) used microsatellite DNA to determine the geographic location of source populations for individual brook trout living in a watershed in New Brunswick, Canada. Brook trout in the headwater streams of the watershed originated from five source populations (Rogers and Curry 2004), indicating that dispersal may play an important role in the demography of headwater population.

We are not aware of any studies from Region 2 that have explicitly tried to assess spatial population structure and dispersal within and among brook trout populations, or analyze the resulting influence of demography. Evidence of these processes from other areas (e.g., Adams 1999 Rogers and Curry 2004), combined with observations of dispersal within headwater streams in the region and effects of immigration on local abundance (Gowan and Fausch 1996a,b, Peterson and Fausch 2003a Peterson et al. 2004) suggests that spatial structure and variation in demographic rates are likely.

Brook trout demographic models from other regions

Demographic models are often developed to help biologists evaluate the status of and risk to species of concern (e.g., as part of a population viability analysis [PVA]; Morris and Doak 2002). Such models can also be used to evaluate the influence of environmental variation and management on species that may not be at risk, but are of considerable economic, ecological, or societal importance. A number of brook trout population models have been published in the past 15 years, and they have included both individual-based (Power and Power 1995, Power 1996, Clark and Rose 1997a,b, Clark et al. 2001) and matrix modeling frameworks (Adams 1999, Marschall and Crowder 2001). Only one of these studies addressed the demography of brook trout in a portion of their introduced range (e.g., Adams 1999 in Montana), and none are specific to Region 2, though one is currently in development (D. Peterson, U.S. Fish and Wildlife Service, unpublished manuscript).

Brook trout population models have been developed for a variety of purposes, but a consistent trait among these diverse models appears to be the sensitivity of population growth to survival of young brook trout. For example, Marshall and Crowder (1996) used a size-classified matrix population model to examine population-level responses of southern Appalachian brook trout to environmental perturbations, including invasion by exotic rainbow trout, decreases in pH, increases in siltation, and increases in angling mortality. They found that population size was most sensitive to changes in survival of brook trout sized 60 to 100 mm, but it was insensitive to egg to fry survival, perhaps because their model included a density-dependent effect at young life stages.

Clark and Rose (1997b) used an individual-based model to assess different management strategies for enhancing brook trout in southern Appalachian streams. They found that strategies that decreased interspecific competition (with rainbow trout) in the age-0 stage (i.e., through electrofishing suppression) would most benefit these stocks when they are sympatric with rainbow trout.

In western North America, Adams (1999) conducted a comprehensive demographic analysis of brook trout in a Montana stream to test hypotheses about their invasions, using a series of matrix models and life stage analysis to examine how spatial variation in demographic rates might produce distribution limits in brook trout. Using a combination of local data (growth, fecundity) and survival estimates from the literature (e.g., McFadden et al. 1967), she concluded that source-sink population dynamics may operate within brook trout populations and affect their distribution limits. Sensitivity analyses indicate that survival from egg to age-0 in fall always had the most influence on population growth rates (λ), and juvenile survival rates contributed more than adult survival to the variance in λ. Maternity rates also influence the variance in λ when spatial variation in vital rates within a stream was considered.

Demographic models for brook trout in Region 2

Model construction: Adams (1999) observed that stream- or regional-specific data are preferable for developing demographic models to predict population trends in brook trout. Survival estimates for stream resident brook trout in western North America and Region 2 were not available at the time of Adams' study, but have since been published (e.g., Peterson et al. 2004). Accordingly, we used these data to construct time- and spatially-invariant matrix population models for unexploited brook trout populations representative of two different life histories (early vs. delayed maturity) observed in Region 2 (**Figure 5**, **Table 1**; Peterson and Fausch 1998, Peterson and Fausch 2000, Kennedy et al. 2003, Peterson et al. 2004). Relative to the early maturity life history (life history 1), the delayed maturity life history (life history 2) is characterized by greater longevity, higher adult survival, and a two-year delay in female maturation. We did not include density-dependence in these models because we were uncertain about how to mathematically represent the effect (e.g., Adams 1999). We recognize that density dependence may be important for young brook trout in some instances (e.g., McFadden 1961, McFadden et al. 1967), so the models we present will overestimate population growth if density-dependence is important. Data for egg-to-age-0 survival and fecundity were not available for Region 2. We used the models to estimate the finite rate of population increase, conducted a basic sensitivity analysis of the two matrices to determine how specific vital rates affect population growth, and briefly examined the demographic implications of the two models. We constructed the models in Microsoft Excel, and matrix analyses were performed with the Excel PopTools add-in (Hood 2004).

Results: Population growth rates (λ) were positive (>1.0) for both models, but the early-maturity model was characteristic of explosive population growth (i.e., 1.21 or 21 percent annual increase; **Figure 6**). Population growth was much lower in the delayed-maturity model

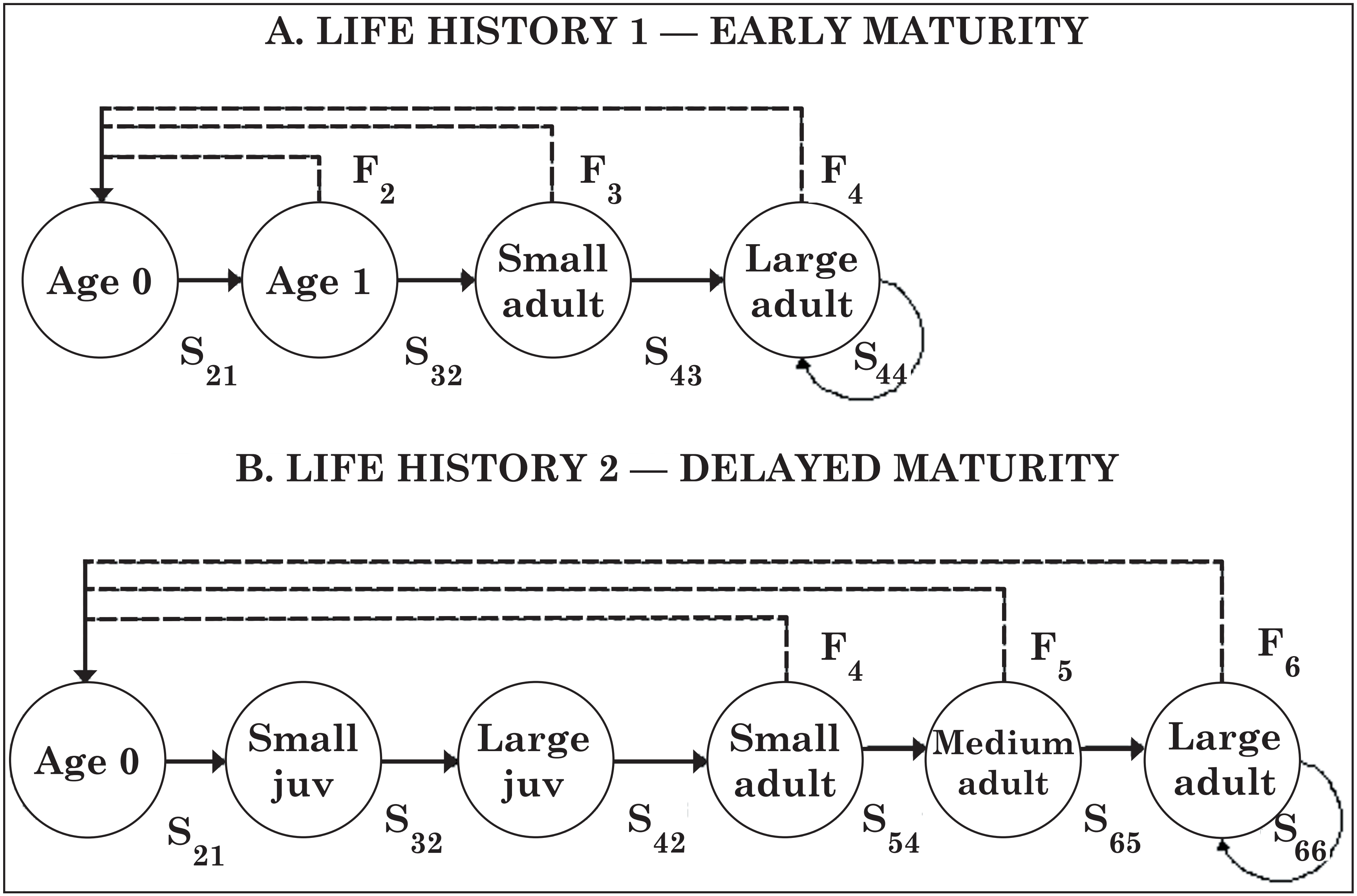

Figure 5. Life-cycle diagrams for two life history types characteristic of stream-resident brook trout in Region 2. Solid arrows and S-variables denote survival probabilities for age-0 and older trout. Dashed lines and F-variables denote reproductive output of mature female brook trout. Relative to life history – early maturity (A), brook trout expressing life history 2 – delayed maturity (B) reach sexual maturity two years later and exhibit greater longevity.

Table 1. Vital rates for brook trout demographic models under two life histories. Both models are female-based and assume annual spawning.

Model element or parameter	Matrix notation	Mean value	Sources
Life history 1 – early maturity			
Age-0 (YOY)	S_{21}	0.323	Peterson et al. (2004)[a]
Age-1 (Subadult)	S_{32}	0.383	Peterson et al. (2004)[a]
Small adult (130-170 mm FL)	S_{43}	0.371	Peterson et al. (2004)[a]
Large adult (171-219 mm FL)	S_{44}	0.371	Peterson et al. (2004)[a]
Age-1 (Subadult) maturity rate (proportion females mature in stage)	—	0.25	Kennedy et al. (2003)[b]
Small adult female maturity rate	—	0.75	Kennedy et al. (2003)[b]
Large adult female maturity rate	—	1.0	Kennedy et al. (2003)[b]
Age-1 (Subadult) fecundity (eggs/female)	—	25	Tripp et al. (1979)[c]
Small adult female fecundity	—	234.5	Tripp et al. (1979)[c]
Large adult female fecundity	—	527	Tripp et al. (1979)[c]
Egg to age-0 survival from spawning to subsequent fall census (S_{egg})	—	0.061[d]	McFadden et al. (1967); Adams (1999)
Age-1 (Subadult) reproductive output (No. of offspring)[e]	F2	0.2	—
Medium adult reproductive output[e]	F3	5.4	—
Large adult reproductive output[e]	F4	18.8	—
Life history 2 – delayed maturity			
Age-0 (YOY)	S_{21}	0.323[f]	Peterson et al. (2004)
Small juvenile (i.e., Age-1, 75-100 mm FL)	S_{32}	0.383[f]	Peterson et al. (2004)
Large Juvenile (101-150 mm FL)	S_{43}	0.383[f]	Peterson et al. (2004)
Small adult (151-175 mm FL)	S_{54}	0.563	Peterson et al. (2004)
Medium adult (176-200 mm FL)	S_{65}	0.563	Peterson et al. (2004)
Large adult (200-250 mm FL)	S_{66}	0.563	Peterson et al. (2004)
Small adult maturity rate	—	0.12	Kennedy et al. (2003)
Medium adult maturity rate	—	0.68	Kennedy et al. (2003)
Large adult maturity rate	—	1.0	Kennedy et al. (2003)
Small adult eggs/female	—	318.5	Tripp et al. (1979)
Medium adult eggs/female	—	493.5	Tripp et al. (1979)
Large adult eggs/female	—	756	Tripp et al. (1979)
Egg to age-0 survival from spawning to subsequent fall census (S_{egg})	—	0.061[d]	McFadden et al. (1967); Adams (1999)
Small adult reproductive output[e]	F_4	1.2	—
Medium adult reproductive output[e]	F_5	10.2	—
Large adult reproductive output[e]	F_6	23.1	—

[a]Survival rates for ages 0 and older brook trout early maturation model (life history 1) were calculated as the mean for two years (1998, 1999; see Appendix B in Peterson et al. 2004). Estimates from 2000 were not included in the matrix model values because they may have been influenced by very high brook trout density.

[b]Maturity rates were estimated using the equations of Kennedy et al. (2003) evaluated at the midpoint of the size range for that life stage. Life history 1 was estimated using equation for the mid-elevation stream, and life history 2 was estimated using the equation for the high-elevation stream.

[c]The number of eggs per female was estimated using the equation of Tripp et al. (1979) at the midpoint of the size range for that life stage.

[d]Egg to age-0 survival from fall spawning to census the following fall, a period of one year (S_{egg}) was estimated as the midpoint of the mean and high values used in the models of Adams (1999; based on data from McFadden et al. 1967),

[e]Reproductive output (F) for a given stage (i) of brook trout is the product of the sex ratio (assumed 50:50), maturity schedule, eggs/female, and survival of eggs to age 0 (S_{egg}). For example, the average reproductive output for small adult brook trout under life history 1 (F_3) = (0.5)(0.75)(234.5)(0.061) = 5.4

[f]Survival estimates for the early life stages in the delayed maturation model are assumed equivalent to the early maturation model, because estimates of age-0 and age-1 survival were not available for brook trout in the high-elevation streams of Peterson et al. (2004). Trout grew more slowly in the high-elevation streams, so large juveniles in the delayed maturation model were assigned survival of 0.383 (rather than 0.563) based on correspondence in size classes with age-1 brook trout in the early maturation model.

A. LIFE HISTORY 1 — EARLY MATURITY

Symbolic matrix

$$\begin{pmatrix} & F_1 & F_3 & F_4 \\ S_{21} & & & \\ & S_{32} & & \\ & & S_{43} & S_{44} \end{pmatrix}$$

Parameters

$$\begin{pmatrix} & 0.2 & 5.4 & 18.8 \\ 0.323 & & & \\ & 0.383 & & \\ & & 0.371 & 0.371 \end{pmatrix} \quad \boldsymbol{\lambda = 1.21}$$

Elasticity

$$\begin{pmatrix} & 0.011 & 0.099 & 0.153 \\ 0.263 & & & \\ & 0.252 & & \\ & & 0.153 & 0.0679 \end{pmatrix}$$

Sensitivity

$$\begin{pmatrix} 0 & 0.070 & 0.022 & 0.099 \\ 0.985 & 0 & 0 & 0 \\ 0 & 0.796 & 0 & 0 \\ 0 & 0 & 0.500 & 0.221 \end{pmatrix}$$

B. LIFE HISTORY 2 — DELAYED MATURITY

Symbolic matrix

$$\begin{pmatrix} & & & F_4 & F_5 & F_6 \\ S_{21} & & & & & \\ & S_{32} & & & & \\ & & S_{43} & & & \\ & & & S_{54} & & \\ & & & & S_{65} & S_{66} \end{pmatrix}$$

Parameters

$$\begin{pmatrix} & & & 1.2 & 10.2 & 23.1 \\ 0.323 & & & & & \\ & 0.383 & & & & \\ & & 0.383 & & & \\ & & & 0.563 & & \\ & & & & 0.563 & 0.563 \end{pmatrix} \quad \boldsymbol{\lambda = 1.02}$$

Elasticity

$$\begin{pmatrix} & & & 1.2 & 10.2 & 23.1 \\ 0.323 & & & & & \\ & 0.383 & & & & \\ & & 0.383 & & & \\ & & & 0.563 & & \\ & & & & 0.563 & 0.563 \end{pmatrix}$$

Sensitivity

$$\begin{pmatrix} & & & 1.2 & 10.2 & 23.1 \\ 0.323 & & & & & \\ & 0.383 & & & & \\ & & 0.383 & & & \\ & & & 0.563 & & \\ & & & & 0.563 & 0.563 \end{pmatrix}$$

Figure 6. Matrix model representation and sensitivity analyses for two life histories characteristic of stream-resident brook trout in Region 2. See Figure 5 for the corresponding life-cycle diagrams. The deterministic estimates of population growth rate (λ = the dominant eigenvalue of the matrix) are presented next to each parameterized matrix. Elasticity values represent the proportional change in λ from a proportional change in a parameter value (S or F), and are scaled to facilitate comparison among vital rates whose values differ in magnitude. For a given matrix, the sum of elasticities sum to 1. Sensitivity values represent the change in ? from an incremental change in a parameter value.

(i.e., 1.02 or 2%). Generation times derived from the matrix models were 3.9 and 6.5 years for the early- and delayed-maturity models, respectively.

Regardless of the life history, population growth was always most sensitive to incremental (sensitivities) or proportional changes (elasticities) in age-0 survival (**Figure 6**). While survival of young trout strongly influenced population growth under both models, adult survival became increasingly important for the delayed-maturity model. For example, the elasticity value of the largest adult stage in the delayed-maturity model was over twice that in the early-maturity model (0.133 vs. 0.0679).

Negligible population growth in the delayed maturity model implies that a decline in any matrix vital rate (survival or reproductive output) or constituent vital rate (spawning frequency, maturity schedule, egg to fry survival) could drive the population into a decline. Some authors have suggested that recruitment may be more sporadic for brook trout in colder, harsher climates (e.g., Kennedy et al. 2003). This would have significant effect on the growth rate of a population with a delayedmaturity life history. For example, if brook trout experienced recruitment failures every other year (by dividing each reproductive output value in the matrix by 2), then the long-term population growth rate for the delayed-maturity population would decline from 1.02 to 0.92 (λ is still >1.0 for early-maturing populations under the recruitment failure scenario). In such cases, immigration may become increasingly important to sustain the local population (Adams 1999).

Small changes in reproductive output and fecundity did not appear to have a strong effect on population growth rates (**Figure 6**). We point out, however, that reproductive output is the product of sex ratio, maturity, eggs per female, and egg-to-age-0 survival (S_{egg}). This final constituent vital rate, in particular, has been shown to be quite variable in natural populations (e.g., McFadden et al. 1967), and small changes in this value can have comparatively large effects on population growth under our models. For example, a 10 percent reduction in egg-to-age-0 survival (from 0.061 to 0.0549) was equivalent to a 10 percent reduction in age-0 survival (from to 0.323 to 0.2907), in that either change reduced λ to 1.18 and 1.00 for early- and delayed-maturity models, respectively. Region-specific data on survival of brook trout from egg through their first year, as well as estimates for juvenile brook trout in colder habitats, are needed to construct more robust matrix models for brook trout in Region 2. We caution that two matrix models presented in this assessment are fairly simple, were intended to provide a quick overview of demographic variability and processes, and should not be over-generalized as representative of all stream resident brook trout in Region 2. Future models should consider density dependence, temporal and spatial variation in vital rates, and the influence of immigration both within and among streams.

Community ecology

Predators

A number of animals are known or suspected predators of brook trout. Mammals, such as mink (*Mustela vison*), and birds, such as mergansers (Power 1980), loons (*Gava immer*), and great blue herons (*Ardea herodius*), (Matkowski 1989) prey upon juvenile brook trout. Larger fish such as northern pike (*Esox lucius*) and yellow perch (*Perca flavescens*) will also prey upon them (Mirza and Chivers 2003). Brown trout are known piscivores and can displace brook trout (e.g., Waters 1983). Interactions with brown trout (both predation and competition) are discussed in the following section (see **Community ecology, Competitors**).

Brook trout rely upon camouflage and hiding behaviors to escape predation. For example, Donnelly and Whorsikey (1991) showed that given time to acclimate to a background before the introduction of a predator (a hooded merganser), juvenile brook trout experienced lower mortality by predation. In 11 to 12 weeks, the brook trout developed more cryptic coloration that allowed them to escape detection.

The use of cover to avoid predation is also important in salmonids. Johnsson et al. (2004) conducted a laboratory experiment using simulated predator attacks and aquaria with limited cover and showed that juvenile brown trout preferred territories with cover and defended them more vigorously than territories without cover. Brown and Smith (1998) found that juvenile rainbow trout conditioned with a combination of pike odor and an alarm pheromone also sought cover when pike odor was introduced into tanks during subsequent test trials. Conditioned fish that received a control treatment of distilled water did not use cover as often and utilized a larger area of the aquarium (Brown and Smith 1998).

Larger-scale experiments also demonstrate that stream salmonids prefer and benefit from habitat complexity and instream structure. Lonzarich and Quinn (1995) conducted an experiment in artificial stream channels to examine use of cover by coho salmon (*Oncorhynchus kisutch*), steelhead, and cutthroat trout. Channels were assigned one of four treatments: deep pools with structure (i.e., cover provided by a piece of wood 1-m in length and 1-m in basal diameter), shallow pools with structure, deep pools without structure, and shallow pools without structure. When fish were allowed to move freely between the treatments, all three species avoided shallow pools without structure. A subsequent experiment measured survival in fish confined to the treatments, and fish confined to deep pools with structure were two to three times more likely to survive than those held in shallow pools without structure. Although avian predator presence was not manipulated, predators such as the belted kingfisher (*Ceryle alcyon*) were common in the watershed, and predation was probably the most common cause of mortality during the experiment. Fausch and Northcote (1992) related the biomass of salmonid species to the presence of large woody debris. They surveyed seven reaches in a small British Columbia stream and found that the three altered sections that had been cleared of large woody debris had approximately one-fifth the salmonid biomass of four relatively unaltered sections that still contained large wood. Brook trout are often associated with overhead cover such as riparian vegetation or large wood (Bossu 1954, Larscheid and Hubert 1992); management activities that reduce these habitat features (e.g., logging or perhaps livestock grazing) may make the species more vulnerable to predation.

Competitors

Demonstrating competition in fishes can be difficult (Fausch 1988), and measurement of its effects can be confounded by the species-specific nature of interaction strength and outcome. Nevertheless, the collective scientific evidence indicates that brook trout interact (competition and predation) with salmonid species that occur in Region 2. Data from both native and introduced ranges indicate that the distribution of brook trout may be strongly influenced by the presence of and interactions with brown trout and rainbow trout, in particular.

Brown trout: Brown trout appear to be more aggressive and competitively dominant to brook trout under certain conditions. In a Michigan stream, Fausch and White (1981) found that brook trout altered their use of resting habitats when brown trout were removed, which implied that brown trout may displace brook trout from more favorable stream positions. Brown trout are also reported to prey on brook trout (Alexander 1977 and Johnson 1981 as cited in Kozel and Hubert 1989b).

Competitive differences and presumed effects of predation by brown trout may lead to longitudinal segregation of the species within a stream or watershed, where brown trout typically predominate at lower elevations (e.g., Kozel and Hubert 1989a,b; Taniguchi et al. 1998, Rahel and Nibbelink 1999). Complete displacement of brook trout by brown trout has been documented. In Region 2, Rahel and Nibbelink (1999) studied trout distributions in the North Platte River system in Wyoming and found a strong negative correlation between the presence of brook trout and the presence of brown trout. Similarly, Kozel and Hubert (1989b) found a negative correlation in the standing stock of brown trout and brook trout in forested stream reaches within Medicine Bow National Forest, Wyoming, whereby brook trout standing stock increased with elevation. In Colorado, Vincent and Miller (1969) found that brown trout (and rainbow trout) were found at lower elevations than brook trout in the Little South Fork Poudre River. They also reported that encroachment by brown trout resulted in the replacement (or near replacement) of brook trout in two tributaries. In a Minnesota stream, Waters (1983) recorded the near complete displacement of brook trout by brown trout over a 15-year period.

However, the outcome of interactions between the two species may depend on abiotic or other factors (i.e., condition specific), and displacement of brook trout by brown trout is not necessarily inevitable. For example, brown trout did not outcompete brook trout at temperatures ≤ 22 °C under laboratory conditions (Taniguchi et al. 1998). Water chemistry can also mediate interactions between two species. Kocovsky and Carline (2005) analyzed Pennsylvania Fish and Boating Commission data from streams throughout Pennsylvania and concluded that base-flow pH was an important predictor of allopatric zones of brook and brown trout and hypothesized that adult brook trout are better competitors at lower pH. However, they also caution that further study (i.e., laboratory tests) would be necessary to confirm this.

Ironically, while displacement by brown trout is a concern within the native range of brook trout (and such displacement occurs in Region 2), the opposite pattern has become a concern in Europe. Introduction of brook trout (from North America) has apparently led to concerns about displacement of native brown trout from some headwater streams in northern Europe (e.g., Öhlund 2002, Korsu et al. 2007). The consistent pattern across both North America and Europe is for brook trout to predominate at higher elevations or in small, headwater streams.

Rainbow trout: Displacement and replacement of brook trout by rainbow trout is a serious management concern within the native range of brook trout, particularly at the southern limits of their distribution (Larson and Moore 1985, Moore et al. 1986, Marschall and Crowder 1996, Clark and Rose 1997a,b). Competition is a presumed mechanism behind this pattern. For example, Lohr and West (1992) studied trout behavior in an Appalachian stream and showed that both juvenile and adult brook trout used deeper water and moved farther from overhead cover upon removal of rainbow trout.

Invading rainbow trout tend to occupy lower stream reaches while brook trout persist in headwater streams, and extensive research has not determined whether this pattern is a result of innate habitat preferences or a result of competition. A simple explanation has been elusive. Magoulick and Wilzbach (1998a) examined competition using paired, single-fish enclosures in a Pennsylvania stream, and they concluded that brook trout and rainbow trout performed equally well (with respect to growth and survival) in downstream, midstream, or headwater habitats. An accompanying laboratory study showed that temperature (13 or 18 °C) and habitat type (pool or riffle) did not modify the outcome of interspecific interactions between juvenile brook and rainbow trout (Magoulick and Wilzbach 1998b). Instead, brook trout captured more food items and grew faster than rainbow trout in all conditions.

There also appear to be exceptions to the general pattern of displacement of brook trout by rainbow trout, and evidence that some invasions have stalled. For example, Strange and Habera (1998) examined rainbow trout invasions in 25 Tennessee streams and found that the zones of interspecific overlap (i.e., sympatry) shifted upstream and downstream between 1978 and 1995, and brook trout distribution remained stable over this regional scale (Strange and Habera 1998).

Further study is required to clarify the mechanisms by which rainbow trout displace brook trout in their native range. Interactions between brook trout and rainbow trout have been little studied in western North America. However, similar longitudinal distribution patterns are often observed, whereby brook trout tend to occur in higher elevation, higher gradient, narrower streams than rainbow trout (e.g., Vincent and Miller 1969, Bozek and Hubert 1992). Benjamin et al. (2007) proposed that biotic resistance from rainbow trout may, in part, limit brook trout invasions in some western U.S. waters, but they found little evidence for biotic resistance in Panther Creek, Idaho. However, given the consistent longitudinal distribution patterns observed for the two species, further investigation of biotic interactions among them is warranted.

Native cutthroat trout: Brook trout are believed to outcompete native cutthroat trout in many instances, and competition has been proposed as a mechanism behind the widespread displacement of cutthroat trout by brook trout (see reviews by Griffith 1988, Dunham et al. 2002, Peterson and Fausch 2003b, Fausch et al. 2006). Resource competition between these species is likely because they have similar ecological niches and diets (Nakano et al. 1998, Dunham et al. 2000).

Typically, brook trout displace cutthroat trout from the downstream reaches of small, headwater streams (Fausch 1989, Adams 1999). Concern over the conservation status of cutthroat trout facing encroachment by brook trout in Region 2 has motivated investigation of competition and its effects (e.g., Cummings 1987, DeStaso and Rahel 1994, Novinger 2000, Peterson et al. 2004). In general, these studies have shown that brook trout are equal or stronger competitors under a range of thermal conditions (DeStaso and Rahel 1994, Novinger 2000), and that survival of age-0 and age-1 brook trout was higher than for cutthroat trout when the two were in sympatry.

In contrast, the observation that brook trout do not always displace cutthroat trout (e.g., Adams et al. 2002, Dunham et al. 2002) or may be less abundant than cutthroat trout (e.g., Fausch 1989) implies that there may be certain conditions under which cutthroat trout may be equal or stronger competitors. Fausch (1989), for example, hypothesized that gradient and temperature may mediate the effects of competition influence distribution of coexisting trout species and explain why cutthroat trout persist in higher-elevation stream reaches. Research into abiotic and biotic factors correlated with occurrence of sympatry between brook trout and cutthroat trout (e.g., J. Dunham personal communication 2007) may clarify where cutthroat trout outcompete brook trout and identify general landscape features where the two species may be likely to coexist.

Disease

Whirling disease, caused by the parasite *Myxobolus cerebralis*, is considered a prominent threat to some salmonid populations in North American. Whirling disease was introduced to North America from Europe and was first discovered in the United States in

Pennsylvania in 1958 (Hoffman 1990). Consequently, North American salmonids did not evolve in the presence of whirling disease, and some species are extremely susceptible to the disease. Symptoms of whirling disease include skeletal deformities and death in severe cases (Gilbert and Granath 2003). Juvenile fish are less resistant to infection by *M. cerebralis*, and whirling disease can severely curtail wild recruitment of fish (Gilbert and Granath 2003).

Brook trout are susceptible to whirling disease, but less so than other salmonids like rainbow trout or steelhead (e.g., O'Brodnick 1979; Whirling Disease Initiative, http://whirlingdisease.montana.edu/about/transmission.htm). In a study from Region 2, 89 percent of brook trout fry held in a field enclosure in the moderately-infected Colorado River died within 4 months of exposure (Thompson et al. 1999). However, there is no evidence that whirling disease is currently affecting wild populations of brook trout in the Region. Infection rates in wild populations may be low because the spring emergence of brook trout fry may coincide with the seasonally low density of the triactinomyxons (TAMS), the life stage of *Myxobolus cerebralis* that infects trout. In heavily infected areas, brook trout fry can exhibit overt clinical signs of the disease such as exopthalmia and skeletal deformities (A. Ficke, personal observation), but the monitoring data are not yet sufficient to determine whether population-level effects of whirling disease are occurring.

Bacterial kidney disease (BKD), caused by the bacterium *Renibacterium salmonarium*, can infect brook trout in Region 2. For example, Mitchum et al. (1979) studied BKD in trout populations in southeastern Wyoming and found that all age classes of brook trout, brown trout, and rainbow trout were infected with the disease and that the proportion of infected brook trout (83 percent of captured individuals) was the highest of the three species. Unlike whirling disease, BKD does not appear to have any intermediate hosts; it is expelled by carriers through feces and is transmitted via the water column (Mitchum and Sherman 1981). Transmission of BKD is horizontal and vertical (i.e., it can be transmitted to adults, juveniles, and eggs) (Bullock and Herman 1988). Bacterial kidney disease was probably introduced into wild populations by the stocking of hatchery fish (Mitchum and Sherman 1981).

Clinical expression of BKD is usually chronic, but acute outbreaks can occur (Mitchum and Sherman 1981), especially with increasing water temperatures (e.g, 13 to 18 °C; Bullock and Herman 1988). Brook trout infected with BKD can also be asymptomatic (Starliper and Tesk 1995).

Most studies of BKD have been conducted with hatchery fish in a laboratory setting (e.g., Bullock and Herman 1988), and little is known about population level effects of the disease. Periodic, BKD-related mortality of brook and brown trout has been observed in streams in southeastern Wyoming (Mitchum et al. 1979), but to our knowledge, there are no other field studies of BKD and brook trout in Region 2.

Conservation Concerns

Potential Threats

Brook trout are often believed to be more tolerant of many anthropogenic disturbances than native cutthroat trout, but they still tend to be more common in forested, relatively undisturbed habitats in western North America (e.g., Schade and Bonar 2005). Moreover, extirpation and decline of brook trout populations in their native range in response to land use impacts (e.g., logging, urbanization, reductions in water quality and quantity) clearly demonstrate that habitat degradation can affect brook trout (Hudy et al. 2005).

Climate change

Climate change and its anticipated effects on water temperature and flow regimes will likely influence brook trout distribution and abundance within Region 2. One general prediction is that the expected warmer water temperatures will reduce the amount of available salmonid habitat. For example, Keleher and Rahel (1996) used a GIS model to predict an average annual warming ranging from 1 to 5° C would reduce the geographic area in the Rocky Mountains containing suitable trout habitat by 16.2 to 68 percent respectively. One implication is that the distribution of coldwater fishes (like brook trout) may shift upward in elevation and/or latitude, which might lead to increased habitat fragmentation. Groundwater temperatures are expected to increase under many climate change scenarios, reducing (cold) thermal refuge to brook trout during the hot, dry summer months (Meisner et al. 1988).

Climate change may result in greater food demands and the higher metabolism of brook trout living in warmer water (Ries and Perry 1995), or increase the growing season in higher latitudes (e.g., Regier and Miesner 1990). Increased water temperatures may also affect the downstream distribution limits of brook trout by facilitating further encroachment by brown trout, which appear to be competitively superior at higher water temperatures (Taniguchi et al. 1998, Nibbelink and Rahel 1999). Conversely, warmer water temperatures at higher elevations may facilitate upstream expansion of brook trout populations into habitats that are thermally unsuitable, or reduce biotic resistance from cutthroat trout if the temperature changes are sufficient to cause a reversal in competitive dominance.

Global climate change may alter the hydrologic cycle and affect habitat suitability for brook trout. Clark et al. (2001) modeled the possible effects of climate change on Appalachian brook trout. The scenarios they explored included an annual temperature increase of 1.5 to 2.5 °C; lower base flows in summer and higher peak flows in spring and fall; higher temperature; altered hydrograph; and episodic flooding that scoured the streambed. The scenario using higher annual temperatures alone resulted in an increase in abundance. However, the two models that incorporated flow regime changes resulted in a complex mosaic of increases and decreases in predicted abundance (Clark et al. 2001).

In Region 2, changes in brook trout distribution and abundance in response to hydrologic changes caused by global warming may be similarly complex. For example, a lower snowpack will likely translate to lower peak flows in the spring (Nijssen et al. 2001), which may decrease mortality of incubating eggs and emergent fry of fall-spawning salmonids in Region 2 (e.g., Latterell et al. 1998, Nehring and Anderson 1993, Fausch et al. 2006). However, it is also possible that precipitation may occur in less frequent and more intense episodes (Palmer and Räisänen 2002), in which case, the hydrograph could become more variable within and between years. Increased frequency of droughts could also impact brook trout populations by reducing food availability or increasing levels of fine sediment (e.g., Hakala and Hartman 2004). Although an altered hydrologic cycle might be detrimental to brook trout populations in the Rocky Mountains, brook trout have been able to establish reproducing populations in a variety of flow regimes and may be resilient to these changes.

The most pronounced effect of climate change could be human response to a new, warmer climate. Increased water diversion (Vörösmarty et al. 2000) and a higher demand for clean hydroelectric power (World Wildlife Fund 2005) could further decrease habitat availability and increase fragmentation for stream salmonids.

Water diversion

Although climate change may affect brook trout in the future, water diversion already impacts populations. Water level affects habitat type and availability (Anderson and Nehring 1985, Pert and Erman 1994, Scruton and Ledrew 1997), and streams require flushing flows to remove fine bed sediments that fill pools and suffocate redds (Scruton and Ledrew 1997, Simpkins and Hubert 2000). Diversion dams and dry channels can also seasonally or permanently fragment habitats. This can disrupt the spatial structure of a population and prevent fish from completing their life cycles (Peter 1998). Small, isolated populations of salmonids confined to short stream reaches often lack access to the resources necessary for persistence (Novinger and Rahel 2003, Young et al. 2005). For example, Morita and Yamamoto (2002) demonstrated that installation of erosion-control dams led to the isolation and occasional extirpation of white-spotted char (*Salvelinus leucomaenis*) populations in Japan. The likelihood of extinction for isolated populations was positively related to the amount of time since the population was isolated and inversely related to the watershed area available above the dam. Similar patterns are expected for isolated populations of other salmonid species (see review by Fausch et al. 2006).

Timber harvest

Timber harvest and road construction can both affect the sediment load and flow regimes of forest streams (see Meehan et al. 1991 for a general review). Logging can alter flow regimes in snowmelt-dominated watersheds by changing the transpiration and water infiltration rates that drive stream flows (Chamberlin et al. 1991). For example, Baxter et al. (1999) found that the density of bull trout spawning redds was negatively correlated with the density of logging roads in a Montana watershed. Removal of trees reduces the availability of large woody debris that stores sediment and provides cover for fish, it allows increased surface erosion, and it allows larger seasonal water temperature fluctuations (Chamberlin et al. 1991). Empirical studies of logging effects on brook trout in the eastern United States have found different population responses at individual study sites. For example, Nislow and Lowe (2003) found more brook trout in recently logged streams, whereas VanDusen and Huckins (2005) observed more brook trout in streams with the longest recovery time since logging.

In Region 2, Eaglin and Hubert (1993) investigated the influence of logging and road construction on stream substrates and trout standing stock (primarily brook trout and brown trout) in the Medicine Bow National Forest, Wyoming. They found that the proportion of logged land and culvert density were both positively related to the amount of fine substrate and substrate embeddedness, and that culvert density was negatively related to trout standing stock. Overall, they concluded that the cumulative effects of logging and associated road construction did appear to affect trout standing stocks negatively.

In the northwestern United States, a number of studies have documented an increase in primary production, macroinvertebrate density, and fish density in logged sites versus those that were uncut or retained a riparian buffer (Newbold et al. 1980, Bilby and Bisson 1992). This suggests that there are a myriad of factors, such as the effect of increased light on trout foraging efficiency (Wilzbach and Cummins 1986), that influence fish populations after a logging-related disturbance. However, streambank instability and high temperatures can reduce the quality of fish habitat in harvested areas on a longer time scale.

Negative effects on salmonid populations are more frequently reported (see Meehan et al. 1991). For example, fish density in a British Columbia stream was much lower in a logged and scarified (all woody debris removed) site than in a reference site or a site where logging debris and existing woody debris had been left in the stream (Young et al. 1999). The long-term effects of historic logging operations are still evident in Region 2. Historically, rivers and streams were used to transport logs from the forest where they were cut to the mills or railheads where they were to be processed. Tie drives, the act of transporting the cut logs downstream, were conducted during the high flows of the spring (Young et al. 1994). Although tie-driving operations ceased in Region 2 in the late 1800's, many streams have not fully recovered: they are still straightened, lacking large woody debris, and characterized by simple habitat and shallow pools (Sedell et al. 1991).

Roads and road crossings

Roads (dirt or paved) can alter surface runoff, increase erosion, and restrict fish passage (Furniss et al. 1991). Ditches and water bars associated with roads in forested areas can affect the delivery of overland water flow to small streams. This, in combination with the bare soil associated with roads, often leads to excessive erosion. Culverts also present problems with respect to proper hydrological function. Often, stream beds will aggrade above a culvert and degrade below it (Furniss et al. 1991). As cited earlier, Eaglin and Hubert (1993) examined effects of logging and road building on trout in the Medicine Bow National Forest, Wyoming, and they found that culvert density was positively related to the amount of fine substrate and substrate embeddedness, and culvert density was negatively related to trout standing stock.

Lack of fish passage at many culverts and road crossings appears to be a significant issue on federal lands in the northwestern United States (U.S. General Accounting Office 2001). For example, USFS Region 1 recently completed a survey and assessment of fish passage at more than 2,800 culverts. They found that 75 percent of these were either total or partial barriers to upstream movement by adult westslope cutthroat trout (Hendrickson et al. 2008). Similarly, a study of a new highway in Labrador, Canada showed that more than half of the culverts inhibited or prevented fish movement (Gibson et al. 2005).

The jumping and swimming ability of brook trout clearly influences which culverts will be partial or total upstream barriers to movement. Kondratieff and Myrick (2006) found that brook trout up to 30 cm in length were unable to jump a barrier over 40 cm in height if the depth of the plunge pool below the barrier was less than 10 cm. The ability of brook trout to pass barriers increases with the depth of the plunge pool. For example, if the plunge pool depth was 40 cm, then individuals >20 cm in length could jump as high as 70 cm. Adams et al. (2000) concluded that falls in excess of 1 m would generally prevent upstream passage by brook trout.

Empirical models and computer simulation tools have been developed for site-specific analysis of fish passage at culverts. For example, Coffman (2005) developed a set of models for fishes common to the Mid-Atlantic Highlands region of the United States that predict whether a culvert is impassable or passable to upstream fish movement based on physical culvert characteristics (e.g, culvert length, inlet elevation, outlet elevation, tailwater control elevation). He then validated and refined the models using a mark-recapture study. In some areas of the United States, the computer software FishXing is used as an assessment tool for evaluation of fish passage physical culvert characteristics (http://www.stream.fs.fed.us/fishxing/index). Like Coffman's models, FishXing uses a set of culvert physical characteristics and associated hydraulic characteristics. FishXing provides an objective, systematic approach for evaluating fish passage, but questions have been raised about the accuracy of the model (Blank et al.

2005). For example, Burford (2005) investigated fish passage in the Clearwater River drainage, Montana, and found through direct assessment of fish movement that FishXing tended to overpredict the number of total fish barriers. He concluded that the model may be more useful in identifying culverts with potential passage concerns than for predicting the amount of passage that actually occurs.

Given the significant effects that habitat fragmentation and population isolation can have on stream-dwelling salmonids (e.g., Morita and Yamamoto 2002; see review by Fausch et al. 2006) and the extent of culvert road crossings on federal lands (U.S. General Accounting Office 2001), direct evaluation of fish passage at culverts in Region 2 is warranted.

Livestock grazing

Livestock grazing can have a number of effects including altered stream morphology (fewer undercut banks, increased width-to-depth ratio) and riparian damage (fewer riparian plants, reduced shade, and soil compaction), and reduced input of terrestrial invertebrates (Platts 1991). These impacts can physiologically stress fish and reduce fish production (Belsky et al. 1999). The effects of grazing are difficult to quantify because many studies have been confounded by other disturbances, difficulty in choosing reference sites, and the lack of pre-grazing data (Platts 1991), but recent data indicate that grazing strategies can have a significant effect on riparian vegetation and salmonid production. For example, a study in western Wyoming compared the high density, short duration (HDSD) rotation, in which cattle graze heavily upon a site for a short time, with a season-long strategy. The HDSD rotation resulted in a two-to-threefold increase in riparian plant biomass and increased input of terrestrial insects into the stream, thus providing more forage for salmonids (Saunders and Fausch In press).

Intensive grazing is an important issue in fisheries management in Region 2 because although riparian areas cover only about 1 percent of western landscapes, cattle densities in these areas are generally high due to water availability and vegetation quality (Armour et al. 1991). The negative effects of poorly managed grazing on riparian and aquatic ecosystems have long been recognized (Platts 1991), and the effects upon riparian subsidies to aquatic food webs should provide additional impetus for the proper management of cattle grazing in Region 2. Grazing rotations that account for physical stream habitat and properly functioning riparian communities should be selected whenever possible.

Acidification

Water pollution can negatively affect brook trout populations. Acidification has had profound effects on brook trout distributions in the eastern United States (Hudy et al. 2005), even though they may be more tolerant of low pH than other salmonids (e.g., brook trout [Kocovsky and Carline 2005]). Atmospheric deposition resulting in acidic waters has not been thoroughly studied in the western United States. The majority of western studies have focused on atmospheric deposition of nutrients (primarily nitrogen) in the Pacific Northwest. Farag et al. (1993) and Campbell et al. (2004) both concluded that atmospheric deposition of acidic compounds is not considered a problem to aquatic environments in the western United States at this time. In the eastern United States, juvenile brook trout appear to be more sensitive to acidification than adults. For example, Van Offelen et al. (1994) conducted a field enclosure experiment with brook trout in a New York lake that experienced acidification of nearshore waters during snowmelt. Juvenile brook trout held in long enclosures extending into deeper water avoided nearshore waters with a pH of 4.73-5.29, and those held in enclosures that confined them to these waters all died (Van Offelen et al. 1994). This suggests that although low pH does not decrease adult survival, it may impact recruitment.

Acid mine drainage (AMD) is one of the most prevalent environmental impacts on aquatic systems from historic mining operations in the Rocky Mountains (Nelson et al. 1991), and the pH of AMD is often low enough to cause mortality or emigration of adult fishes. For example, a survey of 18 impacted sites in seven Colorado streams found that eight of them had a pH ≤ 5 (Niyogi et al. 2001). Water in Cement Creek, a Colorado stream heavily impacted by historic mining, has a pH of 3.8, and the acidity is only ameliorated by mixing with the larger Animas River (Schemel et al. 2000).

Acidic water facilitates dissolution of heavy metals (e.g., copper, cadmium, lead, and zinc) (Hodgson and Levi 1987), making them bioavailable to aquatic organisms. For example, brook trout from polluted sites in the Animas River in Colorado had higher body burdens of heavy metals such as copper than fish captured at less polluted sites (Besser et al. 2001). Though these heavy metals may not be immediately fatal, they are energetically expensive to process and depurate, and this may translate into reduced growth or fecundity (Lewis and Clark 1996). Water pollution may also cause fish to emigrate from suboptimal sites, thereby reducing local abundance.

There is also some evidence that AMD can affect food webs and fish community composition. Nutrient cycling can be slower in mining-impacted streams. For example, Niyogi et al. (2001) showed that because microbial respiration and shredder biomass decreased with increased mining-associated stresses such as dissolved zinc concentrations, leaf litter did not break down as quickly in impacted streams as in relatively pristine streams. This suggests that AMD can result in less productive systems. Also, the possibility that brook trout are more tolerant of acidic or polluted streams than cutthroat trout may elucidate one of the mechanisms by which cutthroat trout have been replaced. The relationship between stream pH and relative competitive ability of brook trout and native cutthroat trout may warrant further study.

Angling

Empirical data from within the native range of brook trout indicate that angler harvest be a major source of mortality in wild populations (e.g., McFadden 1961, McFadden et al. 1967). McFadden et al. (1967) found that angling exploitation was a significant source of mortality for brook trout in Lawrence Creek, Michigan, and concluded that angling was an inverse density-dependent mortality factor in that population.

Angling exploitation may select for specific behavioral traits or growth characteristics in brook trout. For example, Nuhfer and Alexander (1994) conducted a field experiment to test for angler-induced genetic changes in brook trout by stocking fish from three streams (two exploited, one unexploited) into three experimental Michigan Lakes. Although survival rates were not different between the three populations, brook trout from the unharvested population grew faster than those from the other two populations, probably because they allocated more energy towards somatic growth than fish from exploited populations. The fish from the unexploited population were also much more likely to be caught than those from the other populations (Nuhfer and Alexander 1994). In fact, the behavioral changes and altered growth rates demonstrated in this study may make brook trout resilient to heavy angling pressure.

In the western United States, there are little data to indicate that recreational angling is a serious threat to brook trout populations. Brook trout may not be the primary target of recreational fishery, especially where larger-bodied brown trout and rainbow trout are present in waters nearby. In addition, the available data indicate that some brook trout populations can be quite resilient to angling exploitation (cf., Nuhfer and Alexander 1994). For example, Paul et al. (2003) reported on a project designed to enhance native fish populations by targeted, selective angler harvest of nonnative brook trout in a stream in Alberta, Canada, and they found angler harvest failed to reduce local brook trout abundance.

Direct removal and suppression to benefit native species

In some contexts, implementation of conservation actions to benefit native cutthroat trout may be considered a threat to brook trout populations. Brook trout are considered a serious threat to populations of native greenback, Colorado River cutthroat trout, and Rio Grande cutthroat trout in Region 2, and they are often targeted for removal and suppression (e.g., Thompson and Rahel 1996, U.S. Fish and Wildlife Service 1998, Alves et al. 2004, CRCT Coordination Team 2006, Hirsch et al. 2006). Typically managers must remove brook trout from streams containing cutthroat trout if the cutthroat trout population is to persist (Young 2009). The number of techniques available for brook trout and other non-native fish removal is limited, and new approaches have not developed beyond the experimental stage (e.g., pheromone-based removals of brook trout; Young et al. 2003). Probably the most popular approach is chemical treatment with rotenone or antimycin, which have a long history of use in the western United States. Although they are relatively successful, chemical applications are increasingly difficult to conduct because of the growing public controversy associated with their use (Young 2008, 2009). This may involve concerns about chemicals applied to drinking water supplies (Finlayson et al. 2000) or the loss of valued nonnative trout fisheries (Hepworth et al. 2002). Furthermore, federal policy has been inconsistent with regard to where such treatments will be appropriate, and extended delays in these projects from litigation or administrative review have been commonplace (Finlayson et al. 2005). Often, the costs associated with bureaucratic issues have rendered projects in smaller waters uneconomical (Hepworth et al. 2002).

In part because of these problems, managers have increasingly relied on intensive electrofishing to eliminate nonnative trout from streams in which cutthroat trout will be introduced (Brauch and Hebein

2003, Shepard and Nelson 2004). Initially, attempts to remove nonnative trout often employed a single removal conducted in one or a few years, but this was ineffective because even multiple electrofishing passes over a short period of time do not capture all fish present and small numbers of reproducing adults can quickly repopulate a stream (Thompson and Rahel 1996, Shepard et al. 2002, Meyer et al. 2006a). Successful eradication was associated with more intensive removal efforts (6 to 10, 2-pass removals over 1-3 years; Kulp and Moore 2000, Shepard and Nelson 2004). In Young's Greenback cutthroat trout Technical Assessment, non-native species removal and control is examined in depth (Young 2009). As a result, we must commit to restoring cutthroat streams where possible and managing the brook trout fishery in areas that no longer contain native salmonids.

Biological Conservation Status

Abundance and distribution trends

Assessment of the trends in abundance and distribution for brook trout in Region 2 was not practical because of the amount and quality of data that would be needed to demonstrate such trends in a widespread species. Brook trout occur in waters or lands across a range of jurisdictions and ownerships, including private, state, and federal. State and federal land-management agencies, universities, and other organizations may have the data necessary to conduct a trend assessment, but these data would need to be systematically compiled, evaluated for consistency and reliability, and standardized across capture methods prior to any initial analyses.

An additional source of information on the occurrence of brook trout in Colorado and Wyoming may become available in the near future. The U.S. Geological Survey, Rocky Mountain Research Station of the USFS, Colorado State University, and collaborators within state agencies have assembled a large dataset on the occurrence of both native and introduced salmonid species in the western United States (J. Dunham personal communication 2007). The dataset will be used to relate fish distributions to environmental variables (e.g., stream size, water temperature, stream discharge, landscape morphology) derived from a GIS, and should identify large-scale patterns in occurrence of brook trout relative to gradients in these variables. The dataset is not currently available but should eventually be posted on a USFS Web site (e.g., http: //www.fs.fed.us/rm/boise/ index.shtml) or a U.S. Geological Service Web site (e.g., http://fresc.usgs.gov/). This dataset could be used to establish an existing baseline for brook trout occurrence that could be used to evaluate future trends and to predict the impacts of land and water management.

Management and Information Needs of Brook Trout in Region 2

Implications and potential management elements

Brook trout are a widely distributed exotic sport fish that have been present in aquatic systems within Region 2 for more than 125 years. The species may support recreational fisheries in some locations, but the social and economic values of fisheries targeting other nonnative trout (e.g., rainbow trout and brook trout) are generally perceived to be greater. In fact, the contemporary focus on brook trout has been to control existing populations and limit the spread into other waters, especially in Colorado and Wyoming, where the species may come into contact with and have detrimental effects on native fauna such as cutthroat trout. Given the large geographic scale of Region 2, the wide distribution of brook trout (especially in Colorado and Wyoming), the complexity of environmental and human factors that influence its ecology, and the sometimes contradictory societal value placed on an exotic species (i.e., desirable versus undesirable), a general discussion of implications and management elements for the species is beyond the scope of this assessment (cf., Belica 2007). Instead, the following sections provide a few general recommendations for population monitoring and research that would provide information useful to managers and biologists in the Region 2 applicable to a variety of management objectives. A number of related species assessments for native and nonnative salmonids in Region 2 contain useful syntheses and reviews of population monitoring designs and techniques that are directly applicable brook trout (e.g., Pritchard and Cowley 2006, Young 2009). For brevity, we refer readers to these resources rather than repeat that information here.

Tools and practices

Inventory and monitoring of populations

The distribution of brook trout in Region 2 is well-known compared to non-game fish or more cryptic fish species. Additional inventory may still be appropriate in unsurveyed waters or those that have not been surveyed for some time. Development of sampling methods and statistical techniques to estimate species occurrence is currently an active area of research in conservation biology and ecology (e.g., see MacKenzie et al. 2006). However, a higher priority appears to be the compilation and analysis of existing data. Considerable data on the occurrence and relative abundance of brook trout apparently exist within Region 2, but reside with different agencies and organizations. A major focus should be the collation, standardization, validation and analysis of these data to provide a contemporary baseline for the distribution of brook trout within Region 2. As noted earlier, data from brook trout in Colorado and Wyoming are being included in an ongoing effort to identify environmental variables related to the coexistence of native and nonnative fishes in western North America (J. Dunham personal communication 2007). Results of these analyses should provide an initial glimpse at large-scale patterns in occurrence of brook trout relative to environmental gradients or the presence of other species, and the approach could be expanded to other areas within the Region. This type of information would be invaluable for assessing the effects of environmental changes, land use, or other human perturbations on trout populations and aquatic systems.

Monitoring programs for stream fishes generally aim to detect spatial and temporal variation in abundance (Thompson et al. 1998; see review by Young 2008, 2009). Both Young (2008, 2009) and Pritchard and Cowley (2006) review designs and methods that have been used to assess the abundance of stream salmonids. Some of the more important considerations for the design and implementation of any monitoring program that apply to brook trout include:

- considerable variability in the distribution of individuals within a stream or stream network (i.e., spatial variability)
- high variability in abundance of brook trout at any specific location within and between years (i.e., temporal variability)
- precision of abundance estimates using mark-recapture or depletion sampling methods because of incorrect estimation of capture efficiencies
- temporal duration of the monitoring program and frequency of sampling needed to detect changes in abundance and relate those changes to environmental conditions, land use, or interactions with other salmonid species.

One general recommendation is to continue or establish intensive long-term monitoring of populations to provide robust basic demographic and ecological data (addressing the above considerations) for brook trout in the Region (e.g., Riley et al. 1992, Gowan and Fausch 1996a). Long-term studies (≥ 10 yr) are rarely conducted because of expense or other management and research priorities, but they are invaluable sources of information on population structure, temporal variation in abundance, survival and mortality, and fecundity. Indeed, the studies of McFadden et al. (1967) and Hunt (1969) continue to provide some of the basic foundational demographic data incorporated in population models used to explore current management issues like climate change, habitat degradation, and species invasions (e.g., Adams 1999, Clark and Rose 1997a,b; Clark et al. 2001). Technological and statistical methods for studying the population ecology of vertebrates have advanced markedly in the past decade (e.g., Thompson et al. 1998, White and Burnham 1999, White et al. 2006). Although the specific objectives of a long-term monitoring project might relate to a specific issue (e.g., land use, invasive species, climate change), important components should include:

- tagging or marking to follow the fate of individual fish (e.g., passive integrated transponders[PIT tags], visual implant tags, sonic tags)
- active and passive recapture and detection methods (e.g., electrofishing, weirs, stationary PIT-tag antennas, mobile hand-held PIT-tag antennas)
- sampling design appropriate for one of any number of mark-recapture models that would facilitate estimation of abundance, survival, and movement (program MARK, http://www.warnercnr.colostate.edu/~gwhite/mark/mark.htm; see also PWRC Software Archive, Patuxent Wildlife Research Center; U.S. Geological Survey, http://www.mbrpwrc.usgs.gov/software.html).

Information Needs

Brook trout are a relatively well-studied species, but much of this research has been conducted outside of Region 2. For example, a search of the Aquatic Sciences and Fisheries Abstracts database for journal articles on brook trout published between 1970 and 2006 returned 1,339 records, but only 6.5 percent of these included a geographic reference to either Colorado, Wyoming, South Dakota, or Nebraska (search date: 1/19/07, search words: brook trout = "anywhere" plus reference to one of these four states). These results and the review of the literature for this assessment indicated at least a few priority information gaps that should be addressed to assist biologists and managers in Region 2.

First, a regional-scale synthesis of the spatial patterns in brook trout occurrence across abiotic and biotic gradients is warranted. Information on brook trout occurrence in Region 2 exists, but we found that it was not readily accessible for this assessment. The collation and analysis of these data may be a considerable undertaking, but necessary to establish a current benchmark for brook trout distribution that can be used to evaluate the effects of climate change, land use, or other environmental variables. An ongoing project may provide some of this information and guide further investigation (J. Dunham personal communication 2007).

Second, additional region-specific estimates of brook trout vital rates and dispersal are needed to further refine population models, and to make them spatially-explicit. Demographic models have been used to evaluate or predict the effects of climate change and land use on brook trout, or to guide fishery management (e.g., Marschall and Crowder 1996, Clark and Rose 1997a,b; Clark et al. 2001). However, these types of models may be limited by a lack of underlying empirical data, or they may not explicitly consider movement and dispersal (but see Adams 1999). In Region 2, life history variability and dispersal ability are apparently prominent characteristics for some brook trout populations. Additional data on stage- or age-specific survival, immigration and emigration, the existence and nature of density-dependence, as might be collected under the auspices of a long-term mark-recapture monitoring project or experiment, would lead to the development of more robust models that could be applied in this Region.

Third, the consequences of ecological interactions between brook trout and brown trout and rainbow trout given climate change predictions warrant further study. Replacement of brook trout by brown trout and rainbow trout has received considerable attention in eastern North America where brook trout are native, but this has been little studied in western North America (but see Benjamin et al. 2007). Climate change models predict increasing stream temperatures, so it follows that salmonids with higher thermal optima (i.e., brown trout and rainbow trout) may begin to increase their upstream distribution limits and encroach further into habitats currently occupied by cutthroat trout (e.g., McHugh and Budy 2005) or brook trout.

Finally, a multi-scale genetic inventory of wild brook trout populations in Region 2 is warranted. Genetic markers can be used to assess a number of individual and population-level characteristics, including the amount of genetic diversity within a population, the extent of spatial population structure, and levels of differentiation between populations and drainages (Pritchard and Cowley 2006). A genetic inventory and analysis of brook trout in Region 2 might address the ancestry of naturalized brook trout relative to native wild stocks in eastern North America, the extent of gene flow within and among populations, or whether the habitat fragmentation is leading to genetic bottlenecks in isolated populations. These data would be of interest to biologists seeking to understand the population ecology of brook in the context of either managing brook trout populations for a recreational fishery, assessing the impacts of land use, or limiting impacts on native cutthroat trout.

Definitions

Alevin – a newly hatched salmonid that relies on the yolk sac for nutrition.

Allopatric – not overlapping in distribution with another species.

Anadromous – a life history form that uses the ocean for rearing and growth but migrates to streams to spawn.

Anchor ice – submerged ice that is attached to the stream bottom; when dislodged or floating in the water column, often referred to as frazil ice.

Anthropogenic – of human cause or origin.

Benthic – occurring at or pertaining to the bottom of a body of water.

Demographic – pertaining to the study of population statistics, changes, and trends based on various measures of fertility, survival and movement.

Deterministic – referring to events that have no random or probabilistic aspects but proceed in a fixed predictable fashion.

Diel – over a 24-hour period.

Extirpation – loss of a taxon from part of its range.

Fry – an early life stage of a salmonid, after the fish has emerged from the gravel (i.e., after the alevin stage).

Genetic marker – a sequence of DNA occupying a specific location on a chromosome that can be used to address a population genetic question.

Heterozygosity – having two or more alleles (forms of a gene or genetic marker) at a particular locus (portion of a chromosome containing a gene or genetic marker); may apply to an individual or a population.

Homing – returning to reproduce in the same location where born, in contrast to straying.

Hybridization – production of offspring from mating of separate taxa.

Introgression – movement of genetic material from one taxon to another.

Iteroparous – capable of reproducing more than once in a lifetime.

Macroinvertebrates – with respect to fish, usually invertebrates (e.g., insects, spiders, annelids) that are large enough to constitute part of the diet.

Metapopulation – a collection of patches or local populations each of which has some probability of extinction, but which are linked by dispersal (Hanski 1994). Connected patches or populations can be replenished by immigrants in the event of a severe population decline, or refounded in cases of extirpation. Although subpopulations or population segments in specific habitat patches may be extirpated, metapopulation structure theoretically reduces the probability that an entire population goes extinct (den Boer 1968).

Phenotype – the observable characteristics of an organism (e.g., behavior, physiology, morphology, life history, biochemical makeup), as determined by both genes and environmental influences.

Piscivore – feeding on fish.

Plasticity – the production of multiple phenotypes from a single genotype, in response to biotic and abiotic aspects of organisms' environments.

Polymorphism – different forms (i.e., of a gene, behavior, or phenotypic characteristic).

Refugia – typically, habitat sanctuaries from extreme environmental events.

Resident – a life history form that confines its migrations to small- to medium-sized streams.

Riparian – a transitional zone between the aquatic and terrestrial habitats.

S_{egg} **–** for this assessment, survival from spawning in one fall to age-0 the next fall; equivalent to egg-to-age-0 survival.

S_{21} **–** for this assessment, interannual survival from stage 1 to stage 2 (from fall to fall) in the demographic model. In this instance, S_{21} represents survival from age 0 to age 1, or from age 0 in one fall to age 1 the next fall. Similarly, S_{32} represents survival from age 1 to age 2, or from age 1 in one fall to age 2 the next fall.

Salmonid – a member of the family Salmonidae, including trout, charr, salmon, grayling, and whitefish.

Stochastic – random.

Sympatric – co-occurring with a particular species.

Taxon (s.), taxa (pl.) – a taxonomic group of any rank, for example genus, species or subspecies.

Tie-driving – historic logging practice of straightening a river or stream channel before using high spring flows to transport logs downstream to railroad or mill processing site.

Vital rates – demographic characteristics, such as fecundity and age-specific survival, that determine population growth rate.

Young-of-the-year – a fish in its first year of life (age 0).

References

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

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(3):623-638.

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.

Alexander, G.R. 1977. Consumption of trout by large predatory brown trout in the north branch of the Au Sable River. Fisheries Research Report 1855. Michigan Department of Natural Resources. Ann Arbor, MI. 27 pp.

Alexander, G.R. and E.A. Hansen. 1983. Effects of sand bedload sediment on a brook trout population. Fisheries Research Report No. 1906, Michigan Department of Natural Resources, Fisheries Division, Ann Arbor, MI.

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

Allen, G.H. 1956. Age and growth of the brook trout in a Wyoming beaver pond. Copeia 1956(1):1-9.

Alves, J., D. Krieger, and T. Nesler. 2004. Conservation plan for Rio Grande cutthroat trout (*Oncorhynchus clarki virginalis*) in Colorado. Colorado Division of Wildlife, Denver, CO. Available: http://wildlife.state.co.us/Research/Aquatic/CutthroatTrout/CutthroatTrout.htm#RioGrande.

Anderson, R.M. and R.B. Nehring. 1985. Impacts of stream discharge on trout rearing habitat and trout recruitment in the South Platte River, Colorado. F.W. Olson, R.G. White, and R.H. Hamre, editors. Symposium on Small Hydropower and Fisheries. American Fisheries Society, Bethesda, MD.

Armour, C.L., D.A. Duff, and W. Elmore. 1991. The effects of livestock grazing on riparian and stream ecosystems. Fisheries 16(1):7-11.

Armstrong, J.D. and K.H. Nislow. 2006. Critical habitat during the transition from maternal provisioning in freshwater fish, with emphasis on Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Journal of Zoology 269: 403-413.

Avault, J.W.J. 1996. Fundamentals of aquaculture: a step-by-step guide to commercial aquaculture. AVA Publishing Company Inc., Baton Rouge, LA.

Baril, M. and P. Magnan. 2002. Seasonal timing and diel activity of lacustrine brook charr, *Salvelinus fontinalis*, spawning in a lake outlet. Environmental Biology of Fishes 64:175-181.

Baxter, C.V. and F.R. Hauer. 2000. Geomorphology, hyporheic exhange, and selection of spawning habitat by bull trout (*Salvelinus conflentus*). Canadian Journal of Fisheries and Aquatic Sciences 57:1470-1481.

Baxter, C.V., C.A. Frissell, and F.R. Hauer. 1999. Geomorphology, logging roads, and the distribution of bull trout spawning in a forested river basin: implications for management and conservation. Transactions of the American Fisheries Society 128:854-867.

Baxter, C.V., K.D. Fausch, and W.C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201-220.

Baxter, G.T. and M.D. Stone. 1995. Fishes of Wyoming. Wyoming Game and Fish, Cheyenne, WY.

Behnke, R.J. 2002. Trout and salmon of North America. Free Press, New York, NY.

Belica, L. 2007. Brown Trout (*Salmo trutta*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/browntrout.pdf.

Belsky, A.J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54:419-431.

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.

Bernier-Bourgault, I. and P. Magnan. 2002. Factors affecting redd site selection, hatching, and emergence of brook charr, *Salvelinus fontinalis*, in an artificially enhanced site. Environmental Biology of Fishes 64:333-341.

Besser, J.M., W.G. Brumbaugh, T.W. May, S.E. Church, and B.A. Kimball. 2001. Bioavailability of metals in stream food webs and hazards to brook trout (*Salvelinus fontinalis*) in the upper Animas River watershed, Colorado. Archives of Environmental Contamination and Toxicology 40:48-59.

Bilby, R.E. and P.A. Bisson. 1992. Allochtonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540-551.

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 Management on Salmonid Fishes and Their Habitat. Special Publication 19, American Fisheries Society, Bethesda, MD.

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.

Blanchfield, P.J. and M.S. Ridgway. 1999. The cost of peripheral males in a brook trout mating system. Animal Behaviour 57:537-544.

Blank M., J, Cahoon, D. Burford, T. McMahon, and O. Stein. 2005. Studies of fish passage through culverts in Montana. Pages 647-661 *in* C.L. Irwin, P. Garrett, and K.P. McDermott, editors. Proceedings of the 2005 *In*ternational Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC. Available: http://repositories.cdlib.org/cgi/viewcontent.cgi?article=1222&context=jmie/roadeco

Boussu, M.F. 1954. Relationship between trout populations and cover on a small stream. Journal of Wildlife Management 18(2):229-239.

Bozek, M.A. and W.A. Hubert. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. Canadian Journal of Zoology 70:886-890.

Brauch, D.E. and S. Hebein. 2003. Colorado River cutthroat trout management in western Colorado during 1999-2002. Colorado Division of Wildlife, Denver, CO.

Brown, G.E. and R.J.F. Smith. 1998. Acquired predator recognition in juvenile rainbow trout (*Oncorhynchus mykiss*): conditioning hatchery-reared fish to recognize chemical cues of a predator. Canadian Journal of Fisheries and Aquatic Sciences 55:611-617.

Brown, L.E., D.M. Hannah, and A.M. Milner. 2006. Thermal variability and stream flow permanency in an alpine river system. River Research and Applications 22:493-501.

Bullock, G.L. and R.L. Herman. 1988. Bacterial kidney disease of salmonid fishes caused by *Renibacterium salmoninarium*. Fish Disease Leaflet 78, U.S. Fish and Wildlife Service, National National Fish Health Research Laboratory, Kearneysville, VA.

Burford, D.D. 2005. An assessment of culverts of fish passage barriers in a Montana drainage using a multi-tiered approach. Master's Thesis. Montana State University, Bozeman, MT.

CRCT Conservation Team. 2006. Conservation agreement for Colorado River cutthroat trout (*Oncorhynchus clarkia pleuriticus*) in the states of Colorado, Utah, and Wyoming. Colorado Division of Wildlife, Fort Collins, CO. 10 pp. Available: http://wildlife.state.co.us/Research/Aquatic/CutthroatTrout/.

CRCT Coordination Team. 2006. Conservation strategy for Colorado River cutthroat trout (*Oncorhynchus clarkia pleuriticus*) in the states of Colorado, Utah, and Wyoming. Colorado Division of Wildlife, Fort Collins, CO. 24 pp. Available: http://wildlife.state.co.us/Research/Aquatic/CutthroatTrout/.

Campbell, D.H., E. Muths, J.T. Turk, and P.S. Corn. 2004. Sensitivity to acidification of subalpine ponds and lakes in northwestern Colorado. Hydrological Processes 18:2817-2834.

Carlson, S.M. and B.H. Letcher. 2003. Variation in brook and brown trout survival within and among seasons, species, and age classes. Journal of Fish Biology 63:780-794.

Chamberlain, C.B. and W.A. Hubert. 1996. Factors affecting brook trout populations in lakes and reservoirs in Wyoming. Journal of Freshwater Ecology 11(3):301-309.

Chamberlin, T.W., R.D. Harr, and F.H. Everest. 1991. Timber harvest and silviculture. Pages 181-206 *in* W.R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitat. Special Publication 19, American Fisheries Society, Bethesda, MD.

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(2):137-139.

Clark, M.E. and K.A. Rose. 1997a. Factors affecting competitive dominance of rainbow trout over brook trout in southern Appalachian streams: implications of an individual-based model. Transactions of the American Fisheries Society 126:1-20.

Clark, M.E. and K.A. Rose. 1997b. An individual-based modeling analysis of management strategies for enhancing brook trout populations in southern Appalachian streams. North American Journal of Fisheries Management 17: 54-76.

Clark, M.E., K.A. Rose, D.A. Levine, and W.W. Hargrove. 2001. Predicting climate change effects on Appalachian trout: combining GIS and individual-based modeling. Ecological Applications 11(1):161-178.

Coffman, J.S. 2005. Evaluation of a predictive model for upstream fish passage through culverts. MS Thesis. James Madison University, Harrisonburg, VA.

Coleman, M.A. and K.D. Fausch. 2007a. Cold summer temperature regimes cause a recruitment bottleneck in age-0 Colorado River cutthroat trout reared in laboratory streams. Transactions of the American Fisheries Society 136: 639-654.

Coleman, M.A. and K.D. Fausch. 2007b. Cold summer temperature limits recruitment of age-0 cutthroat trout in highelevation Colorado streams. Transactions of the American Fisheries Society 136:1231-1244.

Colorado Division of Wildlife. 2007. Colorado Fishing. Colorado Division of Wildlife, Denver, CO. 88 pp. Available: http://wildlife.state.co.us/RulesRegs/RegulationsBrochures/.

Crespi, B.J. and M.J. Fulton. 2004. Molecular systematics of Salmonidae: combined nuclear data yields a robust phylogeny. Molecular Phylogenetics and Evolution 31:658-679.

Culp, J.M., F.J. Wrona, and R.W. Davies. 1986. Response of stream benthos and drift to fine sediment deposition versus transport. Canadian Journal of Zoology 64:1345-1351.

Cummings, T.R. 1987. Brook trout competition with greenback cutthroat trout in Hidden Valley Creek, Colorado. MS Thesis. Colorado State University, Fort Collins, CO.

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.

Cunjak, R.A. and G. Power. 1987. The feeding and energetics of stream-resident trout in winter. Journal of Fish Biology 31:493-511.

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.

Curry, R.A. and W.S. MacNeill. 2004. Population-level responses to sediment during early life in brook trout. Journal of the North American Benthological Society 23(1):140-150.

Curry, R.A., C. Brady, D.L.G. Noakes, and R.G. Danzmann. 1997. Use of small streams by young brook trout spawned in a lake. Transactions of the American Fisheries Society 126:77-83.

Curry, R.A., D. Sparks, and J. van de Sande. 2002. Spatial and temporal movements of a riverine brook trout population. Transactions of the American Fisheries Society 131:551-560.

Danzman, R.G., R.P. Morgan II, M.W. Jones, L. Bernatchez, and P.E. Ihssen. 1998. A major sextet of mitochondrial DNA phylogenetic assemblages extant in North American brook trout (*Salvelinus fontinalis*): distribution and postglacial dispersal patterns. Canadian Journal of Zoology 76:1300-1318.

Daufresne, M., H. Capra, and P. Gaudin. 2005. Downstream displacement of post-emergent brown trout: effects of development stage and water velocity. Journal of Fish Biology 67:599-614.

De Staso, J.I. III and F.J. Rahel. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. Transactions of the American Fisheries Society 123:289-297.

den Boer, P.J. 1968. Spreading of risk and animal numbers. Acta Biotheoretica 18:165-194.

Donnelly, W.A. and F.G. J. Whorsikey. 1991. Background color acclimation of brook trout for crypsis reduces risk of predation by hooded mergansers *Lophodytes cucullatus*. North American Journal of Fisheries Management 11(2):206-211.

Duffield, R.M. and C.H. Nelson. 1998. Stoneflies (Plecoptera) in the diet of brook trout (*Salvelinus fontinalis* Mitchill) in Libby Creek, Wyoming, USA. Hydrobiologia 380:59-65.

Dunham, J. 2007. Forest and Rangeland Ecosystem Science Center, U.S. Geological Survey. Personal communication with D. Peterson et al. on October 26, 2007.

Dunham, J.B. and G.L. Vinyard. 1997. Relationships between body-mass, population density, and the self-thinning rule in stream-living salmonids. Canadian Journal of Fisheries and Aquatic Sciences 54(5):1025-1030.

Dunham, J.B., M.E. Rahn, R.E. Schroeter, and S.W. Breck. 2000. Diets of sympatric Lahontan cutthroat trout and nonnative brook trout: implications for species interactions. Western North American Naturalist 60(3):304-310.

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.

Dunson, W.A. and J. Travis. 1991. The role of abiotic factors in community organization. The American Naturalist 138(5):1067-1091.

Dynes, J., P. Magnan, L. Bernatchez, and M.A. Rodríguez. 1999. Genetic and morphological variation between two forms of lacustrine brook charr. Journal of Fish Biology 54:955-972.

Eaglin, G. 2007. Fisheries Biologist on Medicine Bow/Routt National Forests. USDA Forest Service. Personal communication.

Eaglin, G.S. and W.A. Hubert. 1993. Effects of logging and roads on substrate and trout in streams of the Medicine Bow National Forest, Wyoming. North American Journal of Fisheries Management 13:844-846.

Einum, S., L. Sundt-Hansen, and K.H. Nïslow. 2006. The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. Oikos 113:489-496.

Essington, T.E., P.W. Sorensen, and D.G. Paron. 1998. High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. Canadian Journal of Fisheries and Aquatic Sciences 55:2310-2316.

Farag, A.M., D.F. Woodward, E.E. Little, B. Steadman, and F.A. Vertucci. 1993. The effects of low pH and elevated aluminum on Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*). Environmental Toxicology and Chemistry 12(4):719-731.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62(3):441-451.

Fausch, K.D. 1988. Test of competition between native and introduced salmonids in streams: what have we learned? Canadian Journal of Fisheries and Aquatic Science 45:2238-2246.

Fausch, K.D. 1989. Do gradient and temperature affect distribution of, and interactions between brook char and other salmonids in streams? Physiology and Ecology 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.

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

Fausch, K.D., C.L. Haskes, and M.G. Parsons. 1988. Models that predict standing crop of fish from habitat variables: 1950-1985. USDA Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-213, Portland, OR. Available: http://www.fs.fed.us/pnw/pubs/pnw_gtr213.pdf.

Fausch, K.D., C. Gowan, A.D. Richmond, and S.C. Riley. 1995. The role of large woody debris in forming salmonid habitat in Colorado Mountain streams. Bulletin Français de Pêche et de la Pisciculture 337/338/339:179-190.

Fausch, K.D., Y. Taniguchi, S. Nakano, G.D. Grossman, and C.R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. Ecological Applications 11(5):1438-1455.

Fausch, K.D., C.E. Torgersen, C.V. Baxter, and H.W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52(6):483-498.

Fausch, K.D., B.E. Rieman, M.K. Young, and J.B. Dunham. 2006. Strategies for conserving native salmonid populations at risk from nonnative invasions: tradeoffs in using barriers to upstream movement. USDA Forest Service, Rocky Mountain Research Station, GTR-RMRS-174, Fort Collins, CO. Available: http://www.fs.fed.us/rm/boise/publications/fisheries/rmrrs_gtr174.pdf.

Finlayson, B.J. and seven others. 2000. Rotenone use in fisheries management: administrative and technical guidelines. American Fisheries Society, Bethesda, MD.

Finlayson, B. and 11 others. 2005. Native inland trout restoration on national forests in the western United States: time for improvement? Fisheries 30(5):10-19.

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. 2007a. *Salmo trutta* × *Salvelinus fontinalis*. USGS Nonindigenous Aquatic Species Database, Gainesville, FL. Available: http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=933, revision date Revision Date: 8/11/2004.

Fuller. 2007b. *Salvelinus fontinalis*. USGS Nonindigenous Aquatic Species Database. Gainsville, FL. Available: http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=939, revision date 4/20/2006.

Fuller, P., L.G. Nico, and J.D. Williams. 1999. Nonindigenous Fishes Introduced into Inland Waters of the United States, Special Publication Number 27. American Fisheries Society, Bethesda, MD.

Furniss, M.J., T.D. Roelofs, and C.S. Yee. 1991. Road Construction and Maintenance. Pages 297-323 *in* W.R. Meehan, editor. Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitat, volume 19. American Fisheries Society, Bethesda, MD.

Geist, D.R. and D.D. Dauble. 1998. Redd site selection and spawning habitat use by fall Chinook salmon: the importance of geomorphic features in large rivers. Environmental Management 22(5):655-669.

Gibson, R.J., R.L. Haedrich, and C.M. Wernerheim. 2005. Loss of fish habitat as a consequence of inappropriately constructed stream crossings. Fisheries 30(1):10-19.

Gilbert, M.A. and W.O.J. Granath. 2003. Whirling disease of salmonid fish: life cycle, biology, and disease. Journal of Parasitology 89(4):658-667.

Gowan, C. and K.D. Fausch. 1996a. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecological Applications 6(3):931-946.

Gowan, C. and K.D. Fausch. 1996b. 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.

Gowan, C. and K.D. Fausch. 2002. Why do foraging stream salmonids move during summer? Environmental Biology of Fishes 64:139-153.

Gowan, C., M.K. Young, K.D. Fausch, and S.C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 51:2626-2637.

Grant, J.W.A. and D.L.G. Noakes. 1987a. Movers and stayers: foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. Journal of Animal Ecology 56:1001-1013.

Grant, J.W.A. and D.L.G. Noakes. 1987b. Escape behaviour and use of cover by young-of-the-year brook trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 44:1390-1396.

Grant, J.W.A. and D.L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Sciences 47:1724-1737.

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

Guffey, S.Z., G.F. McCracken, S.E. Moore, and C.R. Parker. 1999. Management of isolated populations: native southern Appalachian brook trout. Pages 247-265 *in* J. Peine, editor. Ecosystem management for sustainability:

principles and practices illustrated by the regional biosphere reserve cooperatives. CRC Press, Boca Raton, FL.

Habera, J. and S. Moore. 2005. Managing Southern Appalachian brook trout: a position statement. Fisheries 30(7): 10-20.

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.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63(1):151-162.

Harig, A.L. and K.D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecological Applications 12(2):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.

Hayes, J.P., S.Z. Guffey, F.J. Kriegler, G.F. McCracken, and C.R. Parker. 1996. The genetic diversity of native, stocked, and hybrid populations of brook trout in the southern Appalachians. Conservation Biology 10:1403-1412.

Hazzard, A.S. 1932. Some phases of the life history of eastern brook trout, *Salvelinus fontinalis* Mitchill. Transactions of the American Fisheries Society 62:344-350.

Heggenes, J. 1988. Effects of short-term flow fluctuations on displacement of, and habitat use by, brown trout in a small stream. Transactions of the American Fisheries Society 117:336-344.

Heggenes, J. and T. Traaen. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. Journal of Fish Biology 32:717-727.

Hendrickson, S., K. Walker, S. Jacobsen, and F. Bower. 2008. Assessment of aquatic organism passage at road/stream crossings for the Northern Region of the USDA Forest Service. USDA Forest Service, Northern Region. Available: http://www.fs.fed.us/rl/projects/engineering/fish_passage_web.pdf.

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. 2004. Influence of habitat type on food supply, selectivity, and diet overlap of Bonneville cutthroat trout and nonnative brook trout in Beaver Creek, Idaho. North American Journal of Fisheries Management 24:33-40.

Hirsch, C.L., S.E. Albeke, and T.P. Nesler. 2006. Range-wide status of Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*): 2005. Colorado Division of Wildlife, Denver, CO. Available: http://wildlife.state.co.us/Research/Aquatic/CutthroatTrout/.

Hirtzel, S. 2007. Fisheries Biologist, Black Hills National Forest. USDA Forest Service. Personal communication

Hodgson, E. and P.E. Levi. 1987. Modern Toxicology. Appleton & Lange, Norwalk, CT.

Hoffman, G.L. 1990. *Myxobolus cerebralis*, a worldwide cause of salmonid whirling disease. Journal of Aquatic Animal Health 1990(2):30-37.

Hood, G.M. 2004. PopTools version 2.6.2. Available: http://www.cse.csiro.au/poptools.

Hubert, W.A. and H.A. Rhodes. 1989. Food selection by brook trout in a subalpine stream. Hydrobiologia 178:225-231.

Hudy, M., T.M. Thieling, N. Gillespie, and E.P. Smith. 2005. Distribution, status and perturbations to brook trout within the eastern United States. Final report to the steering committee of Eastern Brook Trout Joint Venture. 77 pp. Available: http://www.easternbrooktrout.org/statusta.html.

Hunt, R.L. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. Journal of the Fisheries Research Board Canada 26:1473-1483.

Hutchings, J.A. 1993. Adaptive life histories effected by age-specific survival and growth rates. Ecology 74(3):673-684.

Hutchings, J.A. 1994. Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. Oikos 70:12-20.

Hutchings, J.A. and L. Gerber. 2002. Sex-biased dispersal in a salmonid fish. Proceedings of the Royal Society London B: Biological Sciences 269: 2487-2493.

Hutchings, J.A., A. Pickle, C.R. McGregor-Shaw, and L. Poirier. 1999. Influence of sex, body size, and reproduction on overwinter lipid depletion in brook trout. Journal of Fish Biology 55:1020-1028.

Isaak, D.J. and W.A. Hubert. 2000. Are trout populations affected by reach-scale stream slope? Canadian Journal of Fisheries and Aquatic Sciences 57:468-477.

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.

Johnson, J.H. 1981. Food interrelationships of coexisting brook trout, brown trout, and yearling rainbow trout in the tributaries of the Salmon River, New York. New York Fish and Game Journal 28:88-99.

Johnson, S.L., F.J. Rahel, and W.A. Hubert. 1992. Factors influencing the size structure of brook trout populations in beaver ponds in Wyoming. North American Journal of Fisheries Management 12:118-124.

Johnsson, J.I., A. Rydeborg, and L.F. Sundström. 2004. Predation risk and the territory value of cover: an experimental study. Behavioral Ecology and Sociobiology 56:388-392.

Kanda, N., R.F. Leary, and F.W. Allendorf. 2002. Evidence of introgressive hybridization between bull trout and brook trout. Transactions of the American Fisheries Society 131(4):772-782.

Keeley, E.R. 1998. Behavioural and demographic responses to food and space competition by juvenile steelhead trout (*Oncorhynchus mykiss*). PhD Dissertation, University of British Columbia, Vancouver, Canada.

Keeley, E.R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology 82(5): 1247-1259.

Kehmeier, K. 2007. Fisheries Biologist with Colorado Division of Wildlife. Personal communication.

Keleher, C.J. and F.J. Rahel. 1996. Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a geographic information system (GIS) approach. Transactions of the American Fisheries Society 125:1-13.

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(2): 215-223.

Kocovsky, P.M. and R.F. Carline. 2005. Stream pH as an abiotic gradient influencing distributions of trout in Pennsylvania streams. Transactions of the American Fisheries Society 134:1299-1312.

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(2):361-370.

Korsu, K., A. Huusko, and T. Muotka. 2007. Niche characteristics explain the reciprocal invasion success of stream salmonids in different continents. Proceedings of the National Academy of Sciences of the United States of America 104(23):9725-9729.

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 62:216-219.

Kozel, S.J. and W.A. Hubert. 1989a. Testing of habitat assessment models for small trout streams in the Medicine Bow National Forest, Wyoming. North American Journal of Fisheries Management 9:458-464.

Kozel, S.J. and W.A. Hubert. 1989b. Factors influencing the abundance of brook trout (*Salvelinus fontinalis*) in forested mountain streams. Journal of Freshwater Ecology 5(1):113-122.

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.

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.

Latterell, J.J., K.D. Fausch, C. Gowan, and S.C. Riley. 1998. Relationship of trout recruitment to snowmelt runoff flows and adult trout abundance in six Colorado mountain streams. Rivers 6(4):240-250.

Lennon, R.I. 1967. Brook trout of Great Smoky Mountains National Park. U.S. Fish and Wildlife Service, U.S. Fish and Wildlife Service Technical Paper 15.

Lewis, M.E. and M.L. Clark. 1996. How does streamflow affect metals in the upper Arkansas River? U.S. Geological Survey Fact Sheet FS-226-96, 4 pp. Available: http://pubs.er.usgs.gov/usgspubs/fs/fs22696.

Lindstrom, J.W. and W.A. Hubert. 2004. Ice processes affect habitat use and movements of adult cutthroat trout and brook trout in a Wyoming foothills stream. North American Journal of Fisheries Management 24:1341-1352.

Lohr, S.C. and J.L. West. 1992. Microhabitat selection by brook and rainbow trout in a southern Appalachian stream. Transactions of the American Fisheries Society 121:729-736.

Lonzarich, D.G. and T.P. Quinn. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. Canadian Journal of Fisheries and Aquatic Science 73:2223-2230.

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.

MacKenzie, D.I., J.D. Nichols, J.A. Royle, K.H. Pollock, L.L. Bailey, and J.E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, San Diego, CA.

Magoulick, D.D. and M.A. Wilzbach. 1998a. Are native brook charr and introduced rainbow trout differentially adapted to upstream and downstream reaches? Ecology of Freshwater Fish 1998(7):167-175.

Magoulick, D.D. and M.A. Wilzbach. 1998b. Effect of temperature and macrohabitat on interspecific aggression, foraging success, and growth of brook trout and rainbow trout pairs in laboratory streams. Transactions of the American Fisheries Society 127:708-717.

Marschall, E.A. and L.B. Crowder. 1996. Assessing population responses to multiple anthropogenic effects: a case study with brook trout. Ecological Applications 6(1):152-167.

Matkowski, S.M.D. 1989. Differential susceptibility of three species of stocked trout to bird predation. North American Journal of Fisheries Management 9(2):184-187.

McCracken, G.F., C.R. Parker, and S.Z. Guffey. 1993. Genetic differentiation and hybridization between stocked hatchery and native brook trout in Great Smoky Mountains National Park. Transactions of the American Fisheries Society 122:533-542.

McFadden, J.T. 1961. A population study of the brook trout, *Salvelinus fontinalis*. Wildlife Monographs 7:1-73.

McFadden, J.T., G.R. Alexander, and D.S. Shetter. 1967. Numerical changes and population regulation in brook trout *Salvelinus fontinalis*. Journal of the Fisheries Research Board Canada 24:1425-1459.

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.

McLaughlin, R.L., J.W.A. Grant, and D.L. Kramer. 1994. Foraging movements in relation to morphology, watercolumn use, and diet for recently emerged brook trout (*Salvelinus fontinalis*) in still-water pools. Canadian Journal of Fisheries and Aquatic Sciences 51:268-280.

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.

Meehan, W.R., editor. 1991. Influences of forest and rangeland management of salmonid fishes and their habitats. American Fisheries Society Special Publication 19. Bethesda, MD.

Meisner, J.D., J.S. Rosenfeld, and H.A. Regier. 1988. The role of groundwater in the impact of climate warming on stream salmonines. Fisheries 13(3):2-8.

Meyer, K.A. and J.S. Gregory. 2000. Evidence of concealment behavior by adult rainbow trout and brook trout in winter. Ecology of Freshwater Fish 9:138-144.

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

Mirza, R.S. and D.P. Chivers. 2003. Predator diet cues and the assessment of predation risk by juvenile brook charr: do diet cues enhance survival? Canadian Journal of Zoology 81(1):126-132.

Mitchum, D.L. and L.E. Sherman. 1981. Transmission of bacterial kidney disease from wild to stocked hatchery trout. Canadian Journal of Fisheries and Aquatic Sciences 38:547-551.

Mitchum, D.L., L.E. Sherman, and G.T. Baxter. 1979. Bacterial kidney disease in feral populations of brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and rainbow trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 36:1370-1376.

Modde, T., H.G. Drewes, and M.A. Rumble. 1986. Effects of watershed alteration on the brook trout population of a small Black Hills stream. Great Basin Naturalist 46(1):39-44.

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

Morgan, I.J., L.M. L'Cruz, J.J. Dockray, T.K. Linton, and C.M. Wood. 1999. The effects of elevated summer temperature and sublethal pollutants (ammonia, pH) on protein turnover in the gill and liver of rainbow trout (*Oncorhynchus mykiss*) on a limited food ration. Comparative Biochemistry and Physiology Part A 123:43-53.

Morris, W.F. and D.F. Doak. 2002. Quantitative conservation biology. Sinauer Associates, Inc., Sunderland, MA.

Mullan, J.W., K.R. Williams, G. Rhodus, T.W. Hillman, and J.D. McIntyre. 1992. Production and habitat of salmonids in mid-Columbia River tributary streams. U.S. Fish and Wildlife Service, Monograph I. Leavenworth, WA.

Mullner, S.A. and W.A. Hubert. 2005. Low summer water temperatures influence occurrence of naturalized salmonids across a mountain watershed. North American Journal of Fisheries Management 25:1034-1040.

Nakano, S., S. Kitano, K. Nakai, and K.D. Fausch. 1998. Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native bull charr, S. confluentus, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. Environmental Biology of Fishes 52:345-355.

Nebraska Game and Parks Commission. 2007. 2007 Nebraska Fishing Guide. Nebraska Game and Parks Commission, Lincoln, NE. 36 pp. Available: http://www.ngpc.state.ne.us.

Nehring, R.B. and R.M. Anderson. 1993. Determination of population-limiting critical salmonid habitats in Colorado streams using the Physical Habitat Simulation System. Rivers 4(1):1-19.

Nelson, R.L., M.L. McHenry, and W.S. Platts. 1991. Mining. Pages 425-457 *in* W.R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitat. Special Publication 19. American

Fisheries Society, Bethesda, MD. Newbold, J.D., D.C. Erman, and K.B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Canadian Journal of Fisheries and Aquatic Sciences 37:1076-1085.

Nijssen, B., G.M. O'Donnell, A.F. Hamlet, and D.P. Lettenmaier. 2001. Hydrologic sensitivity of global rivers to climate change. Climatic Change 50:143-175.

Nislow, K.H. and W.H. Lowe. 2003. Influences of logging history and stream pH on brook trout abundance in firstorder streams in New Hampshire. Transactions of the American Fisheries Society 132:166-171.

Niyogi, D.K., W.M. Lewis, Jr., and D.M. McKnight. 2001. Litter breakdown in mountain streams affected by mine drainage: biotic mediation of abiotic controls. Ecological Applications 11(2):506-516.

Northcote, T.G. 1997. Potamodromy in salmonidae—living and moving in the fast lane. North American Journal of Fisheries Management 17:1029-1045.

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

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(3):772-781.

Nuhfer, A.J. and G.R. Alexander. 1994. Growth, survival, and vulnerability to angling of three wild brook trout strains exposed to different levels of angler exploitation. North American Journal of Fisheries Management 14:423-434.

O'Grodnick, J.J. 1979. Susceptibility of various salmonids to whirling disease (*Myxosoma cerebralis*). Transactions of the American Fisheries Society 108:187-190.

Öhlund, G. 2002. Life history and large-scale habitat use of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) – implications for distributional patterns in small lotic systems. MS Thesis, Sveriges Lantsbrusk University, Umeå, Sweden. Available: http://ex-epsilon.slu.se/archive/00001372/01/Ohlund.pdf.

Page, L.M. and B.M. Burr. 1991. A field guide to freshwater fishes of North America north of Mexico. Houghton Mifflin, New York, NY.

Palmer, T.N. and J. Räisänen. 2002. Quantifying the risk of extreme seasonal precipitation events in a changing climate. Nature 415:512-514.

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.

Paul, A.J., J.R. Post, and J.D. Stelfox. 2003. Can anglers influence the abundance of native and nonnative salmonids in a stream from the Canadian Rocky Mountains? North American Journal of Fisheries Management 23:109-119.

Pert, E.J. and D.C. Erman. 1994. Habitat use by adult rainbow trout under moderate artificial fluctuations in flow. Transactions of the American Fisheries Society 123:913-923.

Peter, A. 1998. Interruption of the river continuum by barriers and the consequences for migratory fish. Pages 99-112 *in* M. Jungwirth, S. Schmutz, and S. Weiss, editors. Fish Migration and Fish Bypasses. Fishing News Books, Oxford, England.

Peterson, D.P. and K.D. Fausch. 1998. Effects of nonnative brook trout on Colorado River cutthroat trout populations. Annual report the Colorado Division of Wildlife and U.S. Department of Interior, Central Utah Project Completion Act Office. Fort Collins, CO. 36 pp.

Peterson, D.P. and K.D. Fausch. 2000. Effects of nonnative brook trout on Colorado River cutthroat trout populations. Annual report the Colorado Division of Wildlife; U.S. Department of Interior, Central Utah Project Completion Act Office; and USDA Forest Service, Rocky Mountain Research Station. Fort Collins, CO. 68 pp.

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(3):754-772.

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, R.H., A.M. Sutterlin, and J.L. Metcalfe. 1979. Temperature preference of several species of *Salmo* and *Salvelinus* and some of their hybrids. Journal of Fisheries Research Board Canada 36:1137-1140.

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.

Platts, W.S. 1991. Livestock Grazing. Pages 389-423 *in* W.R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitat. Special Publication 19. American Fisheries Society, Bethesda, MD.

Platts, W.S. and R.L. Nelson. 1988. Fluctuations in trout populations and their implications for land-use evaluation. North American Journal of Fisheries Management 8:333-345.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. Pages 141-203 *in* E.K. Balon, editor. Charrs: Salmonid Fishes of the Genus *Salvelinus*. Dr. W. Junk bv Publishers, The Hague, The Netherlands.

Power, G., R.S. Brown, and J.G. Imhof. 1999. Groundwater and fish—insights from northern North America. Hydrological Processes 13:401-422.

Power, M. 1996. Characterizing cumulative impacts using a brook trout population dynamics model. Ecological Modeling 90:257-270.

Power, M. and G. Power. 1995. A modeling framework for analyzing anthropogenic stresses on brook trout (*Salvelinus fontinalis*) populations. Ecological Modeling 80:171-185.

Pritchard, V.L. and D.E. Cowley. 2006. Rio Grande Cutthroat Trout (*Oncorhynchus clarkii virginalis*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/riograndecutthroattrout.pdf.

Proulx, R. and P. Magnan. 2002. Physiological performance of two forms of lacustrine brook charr, *Salvelinus fontinalis*, in the open-water habitat. Environmental Biology of Fishes 64:127-136.

Quinn, T.P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fisheries Research 18(1-2):29-44.

Quist, M.C., W.A. Hubert, and D.J. Isaak. 2004. Fish assemblage structure and relations with environmental conditions in a Rocky Mountain watershed. Canadian Journal of Zoology 82:1554-1565.

Rabe, F.W. 1970. Brook trout populations in Colorado beaver ponds. Hydrobiologia 35:431-448.

Rahel, F.J. 2000. Homogenization of fish faunas across the United States. Science 288:854-856

Rahel, F.J. and N.P. Nibbelink. 1999. Spatial patterns in relations among brown trout (*Salmo trutta*) distribution, summer air temperature, and stream size in Rocky Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences 56(Suppl. 1):43-51.

Raleigh, R.F. 1982. Habitat suitability index models: brook trout. U.S. Fish and Wildlife Service, FWS/OBS-82/10.24, Fort Collins, CO.

Regier, H.A. and J.D. Miesner. 1990. Anticipated effects of climate change on freshwater fishes and their habitat. Fisheries 15(6):10-15.

Reimers, N. 1979. A history of stunted brook trout populations in an alpine lake. California Fish and Game 65:196-215.

Richmond, A.D and K.D. Fausch. 1995. Characteristics and function of large woody debris in subalpine Rocky Mountain streams in northern Colorado. Canadian Journal of Fisheries and Aquatic Sciences 52:1789-1802.

Ridgway, M.S. and P.J. Blanchfield. 1998. Brook trout spawning areas in lakes. Ecology of Freshwater Fish 1998(7): 140-145.

Rieman, B.E. and J.B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish 6:51-64.

Ries, R.D. and S.A. Perry. 1995. Potential effects of global climate warming on brook trout growth and prey consumption in central Appalachian streams, USA. Climate Research 5(3):197-206.

Riley, S.C. and K.D. Fausch. 1992. Trout population response to habitat enhancement in six northern Colorado streams. Canadian Journal of Fisheries and Aquatic Sciences 52:34-53.

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.

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

Rogers, S.M. and R.A. Curry. 2004. Genetic population structure of brook trout inhabiting a large river watershed. Transactions of the American Fisheries Society 133:1138-1149.

Saltveit, S.J., T. Bremnes, and O.R. Lindås. 1995. Effect of sudden increase in discharge in a large river on newly emerged Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) fry. Ecology of Freshwater Fish 4:168-174.

Satterfield, J.R., Jr., and K.D. Koupal. 1995. Splake as a control agent for brook trout in small impoundments. Pages 431-436 *in* H.L. Schramm, Jr. and R.G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society, Bethesda, MD.

Saunders, W.C. and K.D. Fausch. 2007. Improved grazing management increases terrestrial invertebrate inputs that feed trout in Wyoming rangeland streams. Transactions of the American Fisheries Society 136:1216-1230

Scarnecchia, D.L. and E.P. Bergersen. 1987. Trout production and standing crop in Colorado's small streams, as related to environmental factors. North American Journal of Fisheries Management 7(3):315-330.

Schade, C.B. and S.A. Bonar. 2005. Distribution and abundance of nonnative fishes in streams of the western United States. North American Journal of Fisheries Management 25:1386-1394.

Schainost, S. 2007. Nebraska Game and Parks Commission. Personal communication with D. Peterson, on September 10, 2007.

Schemel, L.E., B.A. Kimball, and K.E. Bencala. 2000. Colloid formation and metal transport through two mixing zones affected by acid mine drainage near Silverton, Colorado. Applied Geochemistry 15:1003-1018.

Schlosser, I.J. and P.L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. American Fisheries Society Symposium 17: 392-401.

Schrank, A.J. and F.J. Rahel. 2004. Movement patterns in inland cutthroat trout: management and conservation implications. Canadian Journal of Fisheries and Aquatic Sciences 61:1528-1537.

Schroeter, R.E. 1998. Segregation of stream dwelling Lahontan cutthroat trout and brook trout: patterns of occurrence and mechanisms for displacement. MS Thesis. University of Nevada, Reno, NV.

Scruton, D.A. and L.J. Ledrew. 1997. A retrospective assessment of the flow regulation of the West Salmon River, Newfoundland, Canada. Fisheries Management and Ecology 4:467-480.

South Dakota Game, Fish, and Parks. 2007. 2007 Fishing Handbook. South Dakota Department of Game, Fish, and Parks, Pierre, SD. 25 pp. Available: http://www.sdgfp.info/Publications/FishingHandbook.pdf.

Sedell, J.R., F.N. Leone, and W.S. Duval. 1991. Transportation of logs and water storage. Pages 325-368 *in* W.R. Meehan, editor. Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitat. Special Publication 19. American Fisheries Society, Bethesda, MD.

Selong, J.H., T.E. McMahon, A.V. Zale, and F.T. Barrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Transactions of the American Fisheries Society 130:1026-1037.

Sexton, K. 2007. Forest Fisheries Biologist for Arapaho/Roosevelt National Forests and Pawnee National Grassland. USDA Forest Service. Personal communication.

Shepard, B.B. and L. Nelson. 2004. Conservation of westslope cutthroat trout by removal of brook trout using electrofishing: 2001-2003. Report to Montana Fish, Wildlife and Parks Future Fisheries Improvement Program.

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.

Sherrill, L.W., III, P.F. Galbreath, and N.D. Adams. 2001. Genetic origin of wild brook trout populations in the Upper French Broad River system, North Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 55:52-62.

Shoshone National Forest. 2000. Forest Plan Monitoring and Evaluation Report: Shoshone National Forest. USDA Forest Service, Cody, WY.

Shuter, B.J. and J.R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119:314-336.

Simpkins, D.G. and W.A. Hubert. 2000. Effects of a spring flushing flow on the distribution of radio-tagged juvenile rainbow trout in a Wyoming tailwater. North American Journal of Fisheries Management 20:546-551.

Skalski, G.T. and J.F. Gilliam. 2000. Modeling diffusive spread in a heterogenous population: a movement study with stream fish. Ecology 81(6):1685-1700.

Sotiropoulos, J.C., K.H. Nislow, and M.R. Ross. 2006. Brook trout, *Salvelinus fontinalis*, microhabitat selection and diet under low summer stream flows. Fisheries Management and Ecology 13:149-155.

Starliper, C.E. and J.D. Tesk. 1995. Relevance of Renibacterium salmoninarum in an asymptomatic carrier population of brook trout, *Salvelinus fontinalis* (Mitchill) Journal of Fish Diseases 18(5):383-387

Stoneking, M., D.J. Wagner, and A.C. Hildebrand. 1981. Genetic evidence suggesting subspecific differences between northern and southern populations of brook trout *Salvelinus fontinalis*. Copeia 1981:810-819.

Strange, E.M., P.B. Moyle, and T.C. Foin. 1993. Interactions between stochastic and deterministic processes in stream fish community assembly. Environmental Biology of Fishes 36(1):1-15.

Strange, R.J. and J.W. Habera. 1998. No net loss of brook trout distribution in areas of sympatry with rainbow trout in Tennessee streams. Transactions of the American Fisheries Society 127:434-440.

Suttle, K.B., M.E. Power, J.M. Levine, and C. McNeely. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecological Applications 14(4):969-974.

Sweka, J.A. and K.J. Hartman. 2001. Influence of turbidity on brook trout reactive distance and foraging success. Transactions of the American Fisheries Society 130:138-146.

Taniguchi, Y. and S. Nakano. 2000. Condition-specific competition: implications for the altitudinal distribution of stream fishes. Ecology 21(7):2027-2039.

Taniguchi, Y., F.J. Rahel, D.C. Novinger, and K.G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences 55:1894-1901.

Thompson, K.G., R.B. Nehring, D.C. Bowden, and T. Wygant. 1999. Field exposure of seven species or subspecies of salmonids to *Myxobolus cerebralis* in the Colorado River, Middle Park, Colorado. Journal of Aquatic Animal Health 11:312-329.

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.

Thompson, W.L., G.C. White, and C. Gowan. 1998. Monitoring Vertebrate Populations. Academic Press, New York, NY. 365 pp.

Toetz, D., M. Muoneke, and J. Windell. 1991. Age, growth and condition of brook trout (*Salvelinus fontinalis*) from an unexploited alpine lake. Northwest Science 65:89-92.

Toetz, D. 1992. Use of mass spectroscopy to investigate the diet of brook trout (*Salvelinus fontinalis*) in an alpine lake. Journal of Freshwater Ecology 7(3):251-256.

Torgersen, C.E., D.M. Price, H.W. Li, and B.A. McIntosh. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. Ecological Applications 9:301-319.

Tripp, D.B., P.T.P. Tsui, and P.J. McCart. 1979. Baseline fisheries investigations in the McLean Creek ATV and Sibbald Flat snowmobile areas, volume I. Prepared for the government of Alberta, Department of Recreation, Parks and Wildlife, Calgary, Alberta, Canada.

U.S. Fish and Wildlife Service. 1998. Greenback cutthroat trout recovery plan. U.S. Fish and Wildlife Service, Denver, CO. Available: http://ecos.fws.gov/docs/recovery_plans/1998/980301.pdf.

U.S. General Accounting Office. 2001. Restoring fish passage through culverts on Forest Service and BLM lands in Oregon and Washington could take decades. GAO-02-136, Washington, D.C. Available: http://www.gao.gov/new.items/d02136.pdf.

U.S. Geological Survey. 2007. *Salvelinus fontinalis* × *namaycush*. USGS Nonindigenous Aquatic Species Database. Gainsville, FL. Available: http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=940, revision date 8/11/2004.

VanDusen, P.J. and C.J.F. Huckins. 2005. Associations among selection logging history, brook trout, macroinvertebrates, and habitat in northern Michigan headwater streams. Transactions of the American Fisheries Society 134:762-774.

Van Offelen, H.K., C.C. Krueger, C.L. Schofield, and C. Keleher. 1994. Survival, distribution, and ion composition in two strains of brook trout (*Salvelinus fontinalis*) fry after exposure to episodic pH depressions in an Adirondack lake. Canadian Journal of Fisheries and Aquatic Sciences 51:792-799.

Vincent, R.E. and W.H. Miller. 1969. Altitudinal distribution of brown trout and other fishes in a headwater tributary of the South Platte River, Colorado. Ecology 50(3):464-466.

Vladykov, V.D. 1956. Fecundity of wild speckled trout (*Salvelinus fontinalis*) in Quebec lakes. Journal of the Fisheries Research Board of Canada 13(6):799-841.

Vörösmarty, C.J., P. Green, J. Salisbury, and R.B. Lammers. 2000. Global water resources: vulnerability from climate change and population growth. Science 289:284-287.

Waters, T.F. 1983. Replacement of brook trout by brown trout over 15 years in a Minnesota stream: production and abundance. Transactions of the American Fisheries Society 112(2a):137-146.

Webster, D.A. and G. Eiriksdottir. 1976. Upwelling water as a factor influencing choice of spawning sites by brook trout (*Salvelinus fontinalis*). Transactions of the American Fisheries Society 105(3):416-421.

Webster, J.J. and K.J. Hartman. 2005. The role of terrestrial invertebrates in allopatric brook trout headwater streams in the central Appalachian mountains. Journal of Freshwater Ecology 21(1):101-107.

White, G.C. and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement:120-138.

White, G.C., W.L. Kendall, and R.J. Barker. 2006. Multistate survival models and their extensions in program MARK. Journal of Wildlife Management 70:1521-1529.

Whitworth, W.E. and R.J. Strange. 1983. Growth and production of sympatric brook and rainbow trout in an Appalachian stream. Transactions of the American Fisheries Society 112:469-475.

Wifpli, M.S. and J. Musslewhite. 2004. Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. Hydrobiologia 520:153-163.

Wiltzius, W.J. 1985. Fish Culture and Stocking in Colorado, 1872-1978. Colorado Division of Wildlife, Fort Collins, CO.

Wilzbach, M.A. and K.W. Cummins. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology 67(4):898-911.

Winkle, P.L. and W.A. Hubert. 1990. Relations between brook trout standing stocks and habitat features in beaver ponds in southeastern Wyoming. North American Journal of Fisheries Management 10:72-79.

Witzel, L.D. and H.R. MacCrimmon. 1983a. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. Transactions of the American Fisheries Society 112:760-771.

Witzel, L.D. and H.R. MacCrimmon. 1983b. Embryo survival and alevin emergence of brook charr, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, relative to redd gravel composition. Canadian Journal of Zoology 61: 1783-1792.

World Wildlife Fund. 2005. Rivers at Risk: Dams and the Future of Freshwater Ecosystems. World Wildlife Fund. 48 pp. Available: http://www.panda.org/dams.

Wyoming Game and Fish. 2007. Wyoming Fishing Regulations. Wyoming Game and Fish, Cheyenne, WY. 33 pp. Available: http://gf.state.wy.us/downloads/pdf/fish/fishregs.pdf.

Young, K.A., S.G. Hinch, and T.G. Northcote. 1999. Status of resident coastal cutthroat trout and their habitat twentyfive years after riparian logging. North American Journal of Fisheries Management 19:901-911.

Young, M. K. 2008. Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/greenbackcutthroattrout.pdf [March 2008].

Young, M.K. 2009. Greenback Cutthroat Trout (*Oncorhynchus clarkii stomias*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/greenbackcutthroattrout.pdf [April 2009].

Young, M.K., W.A. Hubert, and T.A. Wesche. 1989. Substrate alteration by spawning brook trout in a southeastern Wyoming stream. Transactions of the American Fisheries Society 118:379-385.

Young, M.K., D. Haire, and M.A. Bozek. 1994. The effect and extent of railroad tie drives in streams of southeastern Wyoming. Western Journal of Applied Forestry 9:125-130.

Young, M.K., R.B. Rader, and T.A. Belish. 1997. Influence of macroinvertebrate drift and light on the activity and movement of Colorado River Cutthroat trout. Transactions of the American Fisheries Society 126:428-437.

Young, M.K., B.K. Micek, and M. Rathbun. 2003. Probable pheromonal attraction of sexually mature brook trout to mature male conspecifics. North American Journal of Fisheries Management 23:276-282.

Young, M.K., P.M. Guenther-Gloss, and A.D. Ficke. 2005. Predicting cutthroat trout (*Oncorhynchus clarkii*) abundance in high-elevation streams: revisiting a model of translocation success. Canadian Journal of Fisheries and Aquatic Sciences 62:2399-2408.