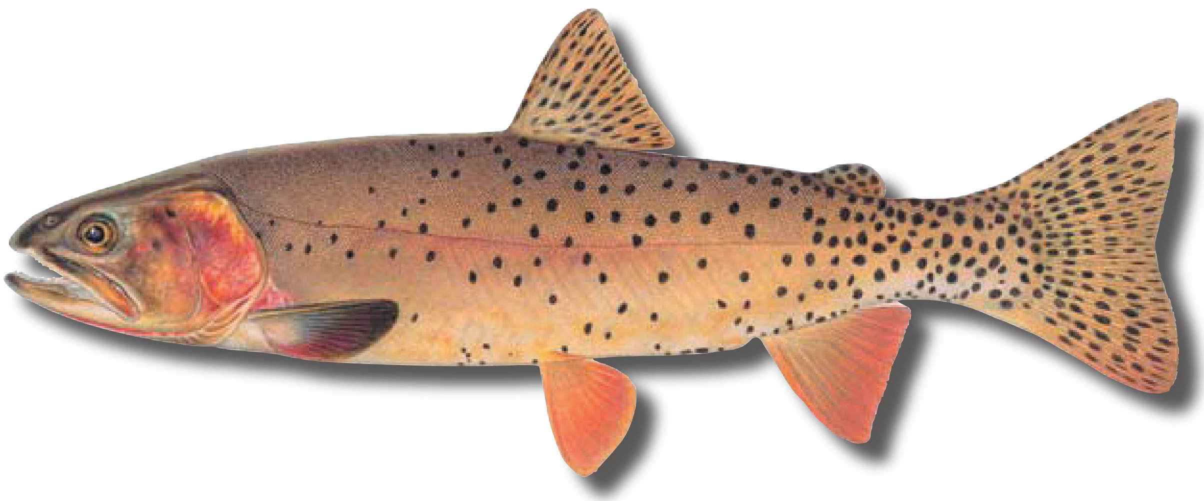
# Yellowstone Cutthroat Trout (*Oncorhynchus clarkii bouvieri*): A Technical Conservation Assessment



**Prepared for the USDA Forest Service, Rocky Mountain Region, Species Conservation Project**

**June 30, 2009**
**Updated version**

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Gresswell, R.E. (2009, June 30). Yellowstone Cutthroat Trout (*Oncorhynchus clarkii bouvieri*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/yellowstonecutthroattrout.pdf [date of access].

## ACKNOWLEDGMENTS

I am grateful to Lynn Kaeding (U.S. Fish and Wildlife Service) and Brad Shepard (Montana Fish, Wildlife, and Parks) for providing published and unpublished information and helpful discussions about Yellowstone cutthroat trout. Travis Horton (Montana Fish, Wildlife, and Parks) provided the 2006 range-wide assessment database assembled by the Yellowstone cutthroat trout Interagency Coordination Group, from which information for all of the tables and maps was obtained. Maps and tables were assembled by Ted Sedell. M.E. Maj, K.A. Meyer, D.D. Miller, D. Scaife, D.S. Winters, W.T. Young, and R.J. Zubik provided comments on earlier versions of this paper.

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Bob Gresswell has been studying habitat relationships and life-history organization of cutthroat trout for more than 30 years. He is currently a research biologist with the USGS Northern Rocky Mountain Science Center in Bozeman, Montana, and he serves as an affiliate assistant professor in the Department of Ecology at Montana State University. Bob's interest in the role of disturbance in shaping the aquatic systems has led to research on the interactions among landscape-scale environmental features, instream habitat characteristics, and cutthroat trout abundance and distribution in watersheds throughout the western USA.

## COVER ILLUSTRATION CREDIT

# Summary of Key Components for Conservation of the Yellowstone Cutthroat Trout

## *Status*

A subspecies of cutthroat trout (*Oncorhynchus clarkii*), the Yellowstone cutthroat trout (*O. c. bouvieri*) was historically found in the Yellowstone River drainage in Montana and Wyoming and in the Snake River drainage in Wyoming, Idaho, Utah, Nevada, and probably Washington. Another subspecies, the finespotted Snake River cutthroat trout (*O. clarkii behnkei*), occurs only within the native range of the Yellowstone cutthroat trout. Because this subspecies cannot currently be distinguished genetically from the Yellowstone subspecies, for the purposes of this review, the finespotted Snake River cutthroat trout is considered as a morphologically divergent ecotype of the more broadly distributed Yellowstone subspecies.

Individual populations of the Yellowstone cutthroat trout have evolved distinct life-history characteristics in response to the diverse environments in which they have been isolated since the last glacial retreat. However, anthropogenic activities have resulted in a substantial reduction in the historical distribution of this subspecies, and many unique local populations have been extirpated. Numerous federal and state resource-management agencies and non-governmental organizations have designated the Yellowstone cutthroat trout as a "species of special concern" or a "sensitive species." A petition for listing as a threatened species under the Endangered Species Act (ESA) was submitted in 1998. Although listing was unwarranted in 2001, a court-ordered status review was initiated in 2005 and published in February 2006. Despite acknowledged declines in the distribution and abundance of Yellowstone cutthroat trout from historical levels (42 percent of its historical range is currently occupied; 28 percent by core, genetically unaltered, populations), the presence of many populations, especially in headwater streams, precluded listing under the ESA. Management actions initiated in the past several decades appeared to stabilize, and occasionally improve, the probability of persistence of the Yellowstone cutthroat trout. At the same time, however, recent events, including the introduction of non-indigenous lake trout (*Salvelinus namaycush*) in Yellowstone Lake, the spread of *Myxobolus cerebralis* (the causative agent of whirling disease), and extended drought in the Intermountain West have resulted in population declines in many areas.

## *Primary Threats*

Primary threats to the persistence of Yellowstone cutthroat trout include (1) non-indigenous species, (2) habitat degradation (e.g., surface water diversions, grazing, mineral extraction, timber harvest, and road building), and (3) global climate change. Many of these threats are geographically ubiquitous, and when systems have been exposed to such threats, restoring altered environments to previous conditions is often impossible. Although each of these threats can be significant alone, in combination, the probability of negative consequences increases substantially. Furthermore, the decline and disappearance of individual populations or assemblages have led to increasing isolation and fragmentation of remaining groups, a fact that increases their susceptibility to the demographic influences of disturbance (both human and stochastic) and genetic factors.

## *Primary Conservation Elements*

Agencies from the five states in the current range of the Yellowstone cutthroat trout (Idaho, Montana, Nevada, Utah, and Wyoming) have the primary responsibility to manage and conserve the subspecies, but in some portions of the range, Tribal governments and the National Park Service have exclusive management jurisdiction. Because the USDA Forest Service, Bureau of Land Management, and other federal agencies manage aquatic habitats, and in some instances fish populations on federal lands, they play an important part in the protection of Yellowstone cutthroat trout. These entities are working with the U.S. Fish and Wildlife Service in the Yellowstone Cutthroat Trout Interagency Coordination Group to maintain status information, promote conservation actions, and gather scientific information appropriate for conserving Yellowstone cutthroat trout.

Yellowstone cutthroat trout populations are managed as sport fish in the states and national parks, regardless of their genetic status. Beyond this basic management strategy, a hierarchical classification for conserving the genetic integrity of cutthroat trout has been developed. Individual groups have been defined as (1) core conservation populations that have not been genetically altered; (2) conservation populations that may be slightly introgressed but have attributes worthy of conservation; and (3) populations managed primarily for their recreational fishery value. Core populations have important genetic value and can be used to develop captive brood stocks, or for direct translocation into historical habitats. Conservation, including potential expansion of core and conservation populations, is integral to management efforts focused on this subspecies.

Currently there are two basic management strategies in use to conserve Yellowstone cutthroat trout. One strategy focuses on preventing risks associated with non-indigenous species (e.g., introgression, disease, predation, and competition) by isolating populations of Yellowstone cutthroat trout. The second strategy concentrates on connecting occupied habitats to preserve metapopulation function and multiple life-history strategies. Because persistence of isolated populations may be greater in the short term, current management of Yellowstone cutthroat trout focuses on isolating individual populations from the threats of non-indigenous fishes and on restoring habitats; however, this strategy implies that humans will act as dispersal agents if a population is extirpated because of stochastic events. In addition, numerous projects are addressing habitat restoration or non-indigenous species removal at a local scale.

A coordinated conservation effort for protection and restoration of Yellowstone cutthroat trout was initiated in 2000 with a Memorandum of Understanding among fish management agencies from the five states where Yellowstone cutthroat trout were historically present (Montana, Idaho, Wyoming, Nevada and Utah) and two federal land management agencies (USDA Forest Service and National Park Service) in the area. The goals of the effort were "to ensure the persistence of Yellowstone cutthroat trout within the historical range" and "to preserve genetic integrity and provide adequate numbers and populations to provide for the protection and maintenance of intrinsic and recreational values" of the subspecies. The objectives included (1) identification of existing populations; (2) protection and enhancement of conservation populations; (3) restoration of extirpated populations; (4) public outreach; (5) data sharing; (6) coordination among agencies; and (7) solutions to common problems and threats. In Montana, Wyoming, and Idaho, Yellowstone cutthroat trout conservation plans have been developed, and in Utah and Nevada, conservation of the subspecies is part of existing trout management plans. Concomitantly, federal land management agencies are working to protect and restore aquatic habitats. Native American tribes with management responsibility for Yellowstone cutthroat trout have developed similar management and conservation actions. Together these groups are working to ensure that angler-related mortality does not negatively affect individual populations, to reduce the genetic introgression (resulting from fish stocking practices and existing feral populations of introduced fishes), and to reduce threats from non-indigenous species. Management activities include population restoration and expansion, and habitat restoration (e.g., riparian fencing, instream habitat improvement, diversion modification, riparian planting, and stream bank stabilization).

The Yellowstone cutthroat trout was historically found in the Yellowstone River drainage in what are now the Shoshone and Bighorn national forests of Region 2 of the USDA Forest Service. Currently, Yellowstone cutthroat trout only occupies approximately 27 percent of its historical range, and it may be impossible to restore the subspecies to 100 percent of its historical range. Furthermore, it appears that the proportion of the range that supports healthy, secure core conservation populations (genetically unaltered and suspected genetically unaltered) is low. Core populations are currently found on 10 percent of its historical range, or 35 percent of the currently occupied range. Only four populations (24 km of stream habitat) exist where non-indigenous salmonids do not occur. Given the array of potential factors that are negatively affecting Yellowstone cutthroat trout populations, persistence of core populations is not certain. Conservation of the subspecies may benefit from a hierarchical approach that includes (1) protection of the strongest core conservation populations; (2) enhancement by reconnecting and replicating the core populations whenever possible; and (3) restoration of populations when practical.

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EDITOR: David Winters, USDA Forest Service, Rocky Mountain Region

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# Introduction

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS). The Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) is included because it is a sensitive species in Region 2. In the National Forest System, a Regional Forester can designate a plant or animal as a sensitive species if the current or predicted downward trends in its abundance and/or habitat capability would significantly reduce its distribution (F.M. 2670.5 (19)). Sensitive species require special management, and therefore, understanding the biology and ecology of these species is critical. The Yellowstone cutthroat trout occurs in only one of the five states comprising Region 2 (Wyoming).

The Yellowstone cutthroat trout has a contiguous native distribution over parts of USFS Regions 1, 2, and 4. Because the subspecies occurs in similar habitats and is subject to similar threats and management activities throughout its range, this assessment is based on information collected from all three Regions; discussion is focused on the status in Region 2 where this is applicable. The broad nature of the assessment leads to some constraints on the specificity of information for particular locales. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production. Scientific and common names of fishes in this report are used according to the latest recommendations from the American Fisheries Society (Nelson et al. 2004).

## *Goal of Assessment*

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based upon knowledge accumulated prior to initiating the assessment. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of the broad implications of that knowledge, and identification of information needs. Specific management recommendations were not developed; however, an ecological background is provided so that the consequences of environmental changes resulting from management actions (i.e., management implications) can be assessed. Recommendations concerning the management of the taxon that were originally proposed elsewhere are noted where applicable.

## *Scope of Assessment*

This assessment examines the biology, ecology, conservation status, and management of the Yellowstone cutthroat with specific reference to the geographic and ecological characteristics of USFS Region 2. Although much of the literature on the subspecies originates from field investigations outside Region 2, this document places that literature in the ecological and social context of the central Rocky Mountains. Similarly, this assessment focuses on the reproductive behavior, population dynamics, and life-history characteristics of the Yellowstone cutthroat trout under the current environment conditions. The evolutionary environment of the species is considered in conducting the synthesis, but it is placed in a current perspective.

In producing the assessment, I relied on peer-reviewed scientific literature, non-peer-reviewed publications, research and management reports, and data collected by management agencies. Not all scientific publications regarding the Yellowstone cutthroat trout were referenced, nor were all published materials considered equally reliable. Peer-reviewed literature was given greater emphasis because it is the accepted standard in science, but non-peer-reviewed publications were used when information was not available elsewhere. Data from the range-wide status assessment completed in 2006 (May et al. 2007) were used to delineate geographic distribution. I did not perform any new statistical analyses. Yellowstone cutthroat trout population data that management agencies have collected but not formally analyzed may represent an additional source of information that has not been fully investigated.

## *Treatment of Uncertainty and Application and Interpretation Limits*

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas about ecological processes are measured against observations, but descriptions of the world are always incomplete and observations are limited. Therefore, we must contend with uncertainty in science. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964), but it is difficult to conduct critical experiments in the ecological sciences. Therefore, observations, inference, heuristic conceptualization, and models must often be used to guide the understanding of ecological relations (Frissell et al. 1997, Hilborn and Mangel 1997).

In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate. Although experiments represent a strong approach to developing knowledge, alternative approaches such as modeling, critical assessment of observations, and inference are accepted as sound approaches to understanding.

### *Treatment of This Document as a Web Publication*

To facilitate access to species assessments in the Species Conservation Project, each is being published on the Region 2 World Wide Web site (http://www.fs.fed.us/r2/projects/scp/assessments/index.shtml). Publication of the documents on the Internet makes them available more rapidly than paper publication and simplifies future revision under guidelines established by Region 2.

### *Peer Review of This Document*

Assessments developed for the Species Conservation Project have been peer-reviewed prior to release on the Web. Region 2 staff conducted the initial internal review. Employing three recognized experts for Yellowstone cutthroat trout, the U.S. Geological Survey, Northern Rocky Mountain Science Center administered additional peer review for this assessment. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

## MANAGEMENT STATUS AND NATURAL HISTORY

### *Management Status*

#### U.S. Fish and Wildlife Service

The U.S. Fish and Wildlife Service (USFWS) received a petition to list Yellowstone cutthroat trout under the Endangered Species Act (ESA) in 1998 (Biodiversity Legal Foundation et al. 1998). Although listing was deemed unwarranted in 2001 (U.S. Fish and Wildlife Service 2001), a court-ordered status review was initiated in 2005. This status review was published February 2006, and despite acknowledged declines in Yellowstone cutthroat trout from historical levels, the presence of many populations, especially in headwater streams, precluded listing the subspecies under the ESA (U.S. Fish and Wildlife Service 2006).

#### USDA Forest Service

The Yellowstone cutthroat trout occurs in the Shoshone and Bighorn national forests in USFS Region 2, in the Gallatin and Custer national forests in USFS Region 1, and in the Bridger Teton and Caribou-Targhee national forests in USFS Region 4. The subspecies is included in the Regional Forester's Sensitive Species List for all three regions. Viability of Sensitive Species is a concern; the Regional Forester proactively selects Sensitive Species to avoid their future listing under the ESA.

#### U.S. Bureau of Land Management

The U.S. Bureau of Land Management (BLM) lists the Yellowstone cutthroat trout as a Bureau-sensitive species, and specifically designates it as a sensitive species in Idaho, Montana, Nevada, Utah, and Wyoming.

#### U.S. National Park Service

In Yellowstone National Park, the National Park Service (NPS) has exclusive jurisdiction for the management of the Yellowstone cutthroat trout, and in both Yellowstone and Grand Teton national parks, the agency is responsible for other natural resources found within the park boundaries. Since 1969, Yellowstone National Park has managed its fishery program to preserve and restore native aquatic fauna and the habitats that support them (Dean and Mills 1971, Gresswell 1986). The Wyoming Game and Fish Department manages fish populations in Grand Teton National Park, including the Yellowstone cutthroat trout (Kiefling 1978).

#### State of Idaho

The American Fisheries Society has designated the Yellowstone cutthroat trout as a "Species of Special Concern - Class A" (Johnson 1987). Idaho Department of Fish and Game recognizes this status for the subspecies and modifies its management practices accordingly (Gresswell 1995).

#### State of Montana

The Montana Department of Fish, Wildlife, and Parks officially recognizes "Species of Special Concern - Class A" designation of the American

Fisheries Society since 1986 (Johnson 1987). More recently, the Yellowstone cutthroat trout was designated as a Tier 1 species in the Comprehensive Fish and Wildlife Conservation Strategy, a plan developed by the Montana Department of Fish, Wildlife, and Parks in collaboration with other state agencies and organizations (Yellowstone Cutthroat Trout Working Group 1994). This designation represents the highest conservation rating for an individual taxon, and Montana Department of Fish, Wildlife, and Parks consequently implements conservation actions that benefit the subspecies.

### State of Nevada

The Yellowstone cutthroat trout has limited distribution in Nevada (May et al. 2003), but the subspecies receives special management consideration by the Nevada Division of Wildlife as a native species.

### State of Utah

Distribution of the Yellowstone cutthroat trout is limited in Utah (May et al. 2003). The subspecies receives special management consideration by the Utah Division of Wildlife Resources as a native species.

### State of Wyoming

The Yellowstone cutthroat trout, including the finespotted Snake River form, is the dominant native trout found in northwestern Wyoming (Wyoming Game and Fish Department 2005). Management of the subspecies has been integral to wild trout management by the Wyoming Game and Fish Department since the 1950's (Wyoming Game and Fish Department 2005). Since 1955, the department has managed the finespotted Snake River cutthroat trout as a separate entity (B. Wichers, 2005 memorandum to W. Fradenberg, U.S. Fish and Wildlife Service, on status review for Yellowstone cutthroat trout).

### Other designations

According to The Nature Conservancy (http://www.natureserve.org/explorer), the Yellowstone cutthroat trout has a Global Heritage Status Rank of G4T2 (a vulnerable subspecies within an apparently secure species). State ranks are S2 (imperiled because of rarity or because of factors making a species vulnerable to extinction) for Idaho, Montana, Utah, and Wyoming, and S1 (critically imperiled because of extreme rarity or because life history characteristics of the species makes it vulnerable to extinction) for Nevada (http://www.natureserve.org/explorer).

## *Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies*

### USDA Forest Service

Most of the management actions completed for Yellowstone cutthroat trout on USFS lands are integrated with the appropriate state fish management agency (e.g., Wyoming Fish and Game Department, Idaho Department of Fish and Game, and Montana Department of Fish, Wildlife, and Parks; K. A. McAllister, 2005 memorandum to W. Fradenberg, U.S. Fish and Wildlife Service, on status review for Yellowstone cutthroat trout). Because the Yellowstone cutthroat trout is on the USFS sensitive species list, Biological Evaluations must include mitigation for projects in the national forest with potential to affect the status of the subspecies (R. Zubik, personal communication, 2007). Furthermore, specific standards and guidelines in national forest land and resource management plans are being modified specifically to protect habitats and populations of Yellowstone cutthroat trout (U.S. Fish and Wildlife Service 2006). These standards and guidelines provide guidance for identifying Federal actions that would benefit subspecies. For example, the Inland Native Fish Strategy has been adopted by the USFS in the Snake River Basin (west of the Continental Divide), and therefore, Yellowstone cutthroat trout are managed by standards and guidelines for protection of biological integrity in watersheds (U.S. Fish and Wildlife Service 2006). In Region 2 of the USFS, the recent revision of the land and resource management plan for the Bighorn National Forest specifically identifies drainages that are suitable for, or that support Yellowstone cutthroat trout for recovery, restoration, and enhancement projects (USDA Forest Service 2006). Although the current land and resource management plan for the Shoshone National Forest does not identify the specific direction for management of the subspecies, the draft revision of the plan emphasizes maintenance of existing populations of Yellowstone cutthroat trout and restoration of genetically pure populations in previously occupied habitat (R. Zubik, personal communication, 2007).

### U.S. Bureau of Land Management

Policy states that the BLM should not fund, authorize, or start any action that would contribute to taxa on the Bureau's sensitive species lists becoming listed as a candidate, threatened, or endangered species under the ESA (Bureau of Land Management 2004). Environmental Assessments are required to analyze the effects of actions on species included on this list. The Inland Native Fish Strategy adopted by the BLM in the Snake River Basin, west of the Continental Divide, provides standards and guidelines for protection of the biological integrity of watersheds (U.S. Fish and Wildlife Service 2006).

### U.S. National Park Service

Almost the entire annual budget for fisheries in Yellowstone National Park focuses on the preservation of Yellowstone cutthroat trout (S. Lewis, 2005 memorandum to W. Fradenberg, U.S. Fish and Wildlife Service, on status review for Yellowstone cutthroat trout). For decades, restrictive angling regulations have been used to protect the subspecies in the park (Gresswell 1986, Gresswell et al. 1994), and beginning in 2001, a mandatory catch-and-release regulation was initiated for Yellowstone cutthroat trout throughout the park. Beginning in 2006, harvest limits were liberalized for non-indigenous species in waters where they are sympatric with the native cutthroat trout. Following the discovery in 1994 of illegally introduced non-indigenous lake trout in Yellowstone Lake (Kaeding et al. 1996), an intensive gillnetting operation was initiated to reduce predation on Yellowstone cutthroat trout in the lake (Koel et al. 2005). In 2005, a program was initiated to identify potential watersheds for reintroducing native Yellowstone cutthroat trout into the northern portion of the park.

### State of Idaho

The Idaho Department of Fish and Game has recently developed a Management Plan for the Conservation of Yellowstone Cutthroat Trout in Idaho (Idaho Department of Fish and Game 2007). The goal of the plan is to provide a management framework to ensure the long-term persistence of the subspecies at levels capable of providing angling opportunities. It focuses on the current range of Yellowstone cutthroat trout in Idaho, and those parts of the historical range where restoration is practical. The plan includes status assessment of Yellowstone cutthroat trout populations in Idaho, including abundance, trends, and genetic status. It also defines each of 13 Geographic Management Units and describes appropriate management strategies for each (Idaho Department of Fish and Game 2007a).

### State of Montana

The Montana Department of Fish, Wildlife, and Parks has played a leadership role in the protection and restoration of the Yellowstone cutthroat trout in the state of Montana, and numerous federal and state agencies and non-governmental groups have been working together with the agency in a coordinated manner. An interagency conservation agreement for Yellowstone cutthroat trout in Montana was completed in September 2000 (Montana Department of Fish, Wildlife, and Parks 2000). This agreement was revised and reauthorized in 2007. In 2005, an update of distribution and genetic status information for fluvial populations in the state was initiated (Shepard and Snyder 2005) for inclusion of the updated range-wide assessment of Yellowstone cutthroat trout (May et al. 2007). Surveys to refine information concerning the distribution and genetic status of Yellowstone cutthroat trout populations in Montana are ongoing. Management emphasis includes protecting currently pure populations, expanding current distribution of the subspecies, and removing the threats imposed by habitat degradation (Montana Department of Fish, Wildlife, and Parks 2000).

### State of Wyoming

Yellowstone cutthroat trout, including the finespotted Snake River form, is the dominant native trout found in northwestern Wyoming (Wyoming Game and Fish Department 2005). Management of the subspecies has been an integral aspect of wild trout management by the Wyoming Game and Fish Department since the 1950's (Wyoming Game and Fish Department 2005). Beginning in 1955, the department managed the finespotted Snake River cutthroat trout as a separate entity (B. Wichers, 2005 memorandum to W. Fradenberg, U.S. Fish and Wildlife Service, on status review for Yellowstone cutthroat trout). Management has focused on genetic integrity, habitat management, recovery projects using selected stocks, education and outreach, and fishing regulations (Wyoming Game and Fish Department 2005). Special angling regulations, some dating back to the 1960's, were initiated in the relevant fish management regions (Cody, Jackson, and Lander) to protect Yellowstone cutthroat trout from overharvest. Difficult access and perceived low angler use have precluded restrictive angling regulations in the Sheridan Fish Management Region.

### Multiparty agreements

The Yellowstone Cutthroat Interagency Coordination Group was formed in 2000 to insure persistence of the Yellowstone cutthroat trout throughout the historical range (Anonymous 2000). Signatories include Grand Teton National Park, Idaho Department of Fish and Game, Nevada Division of Wildlife, Montana Fish Wildlife and Parks, USDA Forest

Service, Utah Division of Wildlife Resources, Wyoming Game and Fish Department, and Yellowstone National Park. The goal of the group includes management to preserve genetic integrity of the Yellowstone cutthroat trout and to provide sufficient numbers and populations to provide for protecting and maintaining intrinsic and recreational values associated with the subspecies. Specific objectives include (1) identifying all existing populations in the historical range of Yellowstone cutthroat trout and maintaining a database of current distribution; (2) securing and enhancing conservation populations; (3) increasing the number of populations by restoring historical populations in the native range; (4) implementing a public outreach program to enlist support for conservation of the Yellowstone cutthroat trout; (5) developing the means to summarize and share existing information concerning distribution, genetic status, and conservation accomplishments across jurisdictions; (6) conducting meetings to share information and discuss problems associated with conservation of the subspecies; and (7) achieving objectives through independent activities and programs by individual agencies and communicating successes and failures to promote cooperation for solving common problems and threats (Anonymous 2000).

In 2001, the group developed the first comprehensive range-wide status assessment for Yellowstone cutthroat trout (May et al. 2003). All Yellowstone cutthroat trout populations that had been identified in the historical range of the subspecies were included, and it was based on the highest quality and most current scientific data collected by state, federal, tribal, and non-governmental biologists (M. J. Hagener, 2005 memorandum to W. Fredenberg, U.S. Fish and Wildlife Service, on status review for Yellowstone cutthroat trout). To assess changes in distribution and genetic status of Yellowstone cutthroat trout populations since the initial comprehensive assessment, a status update was completed in 2006 (May et al. 2007). The updated review included an evaluation of potential population risks resulting from disease, summary of management actions associated with the maintenance of genetic integrity, and a general assessment of population status for each conservation population of Yellowstone cutthroat trout (May et al. 2007).

In 2000, a cooperative agreement for the conservation of Yellowstone cutthroat trout in Montana was adopted by the Crow Tribe; Montana Department of Fish, Wildlife, and Parks; Montana Department of Environmental Quality; Montana Department of Natural Resources and Conservation; USDA Forest Service, Northern Region, Gallatin and Custer national forests; U.S. Bureau of Land Management - Montana; U.S. Fish and Wildlife Service; U.S. Bureau of Indian Affairs; and Yellowstone National Park. This interagency agreement provides a mechanism for conservation of Yellowstone cutthroat trout in Montana. The agreement has a five-year duration, and reauthorization is scheduled for 2009.

### Management of introgressed populations

Because hybridization is an important issue for the conservation of cutthroat trout subspecies, seven western state fish and wildlife management agencies have developed a common strategy for the management of hybridized populations (Utah Division of Wildlife Resources 2000). According to this protocol, management is divided among core populations, conservation populations, sportfish populations, and status unknown populations. Core populations are genetically unaltered ($<1$ percent introgression) and represent the historical genome of the subspecies of interest. Conservation populations were defined as $\leq$ 10 percent introgressed; however, it was recognized that some populations $>10$ percent hybridized might have significant conservation value if they have unique ecological, genetic, or behavioral attributes. For the purposes of the status assessment for Yellowstone cutthroat trout, conservation populations included core conservation populations (genetically unaltered) and introgressed populations (i.e., $\geq 1$ to $\leq 25$ percent introgression) that displayed unique ecological, genetic, or behavioral attributes (May et al. 2003). Fish with $>25$ percent introgression were classified for recreational value only, and they were not included as conservation populations. The Yellowstone Cutthroat Trout Interagency Coordination Group for management, conservation, and restoration of the subspecies has adopted these definitions.

## *Biology and Ecology*

### Systematics and general species description

The Yellowstone cutthroat trout is one of 14 subspecies of cutthroat trout (*Oncorhynchus clarkii*, Order Salmoniformes, Family Salmonidae; Nelson et al. 2004) suggested by Behnke (1988). It is classified among the four major cutthroat trout subspecies (Behnke 1988, 1992) and is one of the most abundant and geographically widespread (Gresswell 1995, May 1996, May et al. 2007). Although the Yellowstone cutthroat trout differs from the finespotted Snake

River cutthroat trout (*O. c. behnkei*) by spotting pattern (Behnke 2002), the two subspecies currently cannot be differentiated genetically.

According to Behnke (1992), the Yellowstone cutthroat trout is characterized by medium-large spots with rounded edges that are usually focused posteriorly. Coloration is highly variable, but the body is usually yellowish brown, silvery, or brassy (Behnke 1992). In Yellowstone Lake, most silvery colored individuals are females or immature males; mature males are usually darker (R. Gresswell, unpublished data). Bright colors are common on individuals (especially on large males) collected from spawning migrations in tributaries of Yellowstone Lake (R. Gresswell, unpublished data). Behnke (1992) reports vertebrae 60-63 (typically 61-62); lateral-line scales 150-200 (typically 165-180); pyloric caeca 25-50 (typically 35-43); gill rakers 17-23 (typically 19-20, but Yellowstone Lake 18-23); and 20 (mean) basibranchial teeth from Yellowstone Lake specimens.

Systematists do not agree on the evolutionary history of cutthroat trout (Behnke 1992, Stearley 1992, Smith et al. 2002), but fossil evidence suggests many species of western trout (including cutthroat trout) originated in the Great Basin during the Miocene (Stearley and Smith 1993, Smith et al. 2002). In fact, the change of the genus name for Pacific trout (including cutthroat trout, rainbow trout [*Oncorhynchus mykiss*], Gila trout [*O. gilae*], and golden trout [*O. mykiss* spp.]) from *Salmo* to *Oncorhynchus* (Smith and Stearley 1989) was based on fossils. In the literature published prior to 1989, cutthroat trout were classified as *S. clarki*. Another potentially confusing taxonomic modification occurred recently when the species name for cutthroat trout was changed from *clarki* to *clarkii* (Nelson et al. 2004).

Diploid chromosome number for Yellowstone cutthroat trout (64) is the same for all of the Snake River-Bonneville Basin-Colorado River subspecies (including Bonneville [*Oncorhynchus clarkii utah*], Colorado River [*O. c. pleuriticus*], greenback [*O. c. stomias*], Rio Grande [*O. c. virginalis*], and the extinct yellowfin [*O. c. macdonaldi*] cutthroat trouts; Behnke 1992). Mitochondrial DNA evidence (Smith et al. 2002) suggests that cutthroat trout diverged from rainbow trout about 8 million years before present (ybp; assuming rates of molecular evolution of approximately 0.05% sequence per million years). Great Basin cutthroat trout appear to have separated from the westslope cutthroat trout (*O. c. lewisi*) (Columbia River) and the Snake-Yellowstone-Bear River group about 4-2 million ybp. Bear River (northern Bonneville) cutthroat (*O. c. utah*) trout separated from the Snake River group about 700,000 ybp (Smith et al. 2002).

According to Behnke (1992), rainbow trout replaced Yellowstone cutthroat trout in the Columbia River Basin below Shoshone Falls on the Snake River sometime after a late-glacial flood event formed the falls (14,500 ybp; Oviatt et al. 1992). Because the Yellowstone cutthroat trout was absent from high-elevation drainages during periods of Pleistocene glaciation, the most recent invasion of the Yellowstone subspecies into the Yellowstone River drainage is associated with the retreat of glacial ice that occurred about 12,000 ybp (Richmond and Pierce 1972). This late Pleistocene range constriction appears to have significantly influenced the current genetic structure of the subspecies.

Yellowstone cutthroat trout can be genetically differentiated from rainbow trout by three genetic techniques (Campbell et al. 2002). For example, allozyme analysis provides at least 10 loci that are diagnostic between the two species (Leary et al.1987, Allendorf and Leary 1988, Leary et al. 1989). Nuclear and mitochondrial DNA can be extracted from small amounts of tissue, and both can be used to differentiate cutthroat and rainbow trout (Campbell et al. 2002). These techniques are also useful for determining hybridization between the two species and among some cutthroat trout subspecies (e.g., westslope, Yellowstone, and Rio Grande cutthroat trouts; Leary et al. 1995).

Metapopulations of Yellowstone cutthroat trout evolved unique life-history characteristics in response to environmental variability and isolation that followed late Pleistocene glaciation (Gresswell et al. 1994). Historically, one of the largest metapopulations occurred in Yellowstone Lake, and an extensive hatchery operation on the lake from 1899 to 1957 led to the worldwide distribution of this form of the subspecies (Varley and Gresswell 1988). Although the information concerning the subspecies is most abundant for the Yellowstone Lake, where invertebrates are the primary food of mature Yellowstone cutthroat trout (Irving 1954, Benson 1961, Jones et al. 1990), piscivory is common in Heart Lake (Snake River drainage, Yellowstone National Park) where the metapopulation co-evolved with seven other fish species (Gresswell et al. 1994). The fluvial metapopulation of Yellowstone cutthroat trout in the Yellowstone River below the

Upper and Lower falls in Yellowstone National Park has persisted despite the introduction and establishment of non-indigenous salmonids (Clancy 1988).

## Distribution and abundance

Fossil evidence suggests that fish species distributions continually vary at geologic time scales (Smith et al. 2002). For example, Behnke (1992) hypothesized that the Yellowstone cutthroat trout once occupied the entire Snake River drainage, but subsequently, rainbow trout replaced the subspecies below Shoshone Falls and rainbow trout and westslope cutthroat trout replaced Yellowstone cutthroat trout in the Salmon and Clearwater drainages. To investigate more recent changes, May et al. (2003) suggested 1800 (approximate time of European settlement of the interior portions of the western United States) as a reasonable reference year for establishing the historical range of Yellowstone cutthroat trout. At that time, the Yellowstone cutthroat trout was found in the Yellowstone River drainage in Montana and Wyoming and portions of the Snake River drainage in Wyoming, Idaho, Nevada, Utah, and possibly Washington (Behnke 1992). Using the distribution boundaries originally proposed by Behnke (1988), Varley and Gresswell (1988) estimated that Yellowstone cutthroat trout historically occupied about 24,000 km of stream habitat and an area of about 44,500 ha of lakes. Recent analysis using an updated hydrography and advanced mapping tools yielded a more precise estimate of historically-occupied fluvial (approximately 27,400 km) and lake (approximately 50,500 ha) habitat (May et al. 2007).

Introduction of non-indigenous fishes (resulting in hybridization, predation, disease, and interspecific competition), habitat degradation (e.g., agricultural practices, water diversions, grazing, mineral extraction, and timber harvest), and angler harvest have resulted in widespread declines in population distribution and abundance of Yellowstone cutthroat trout. Varley and Gresswell (1988) estimated that genetically unaltered populations of Yellowstone cutthroat trout occurred in approximately 10 percent of the historical stream habitat (2,400 km) and about 85 percent of the historical lacustrine habitat (38,500 ha); however, these estimates were based largely on the potential for introgression by transplanted rainbow trout or other cutthroat trout subspecies.

Recent studies with a strong empirical basis provide more optimistic estimates. For example, Thurow et al. (1997) reported that Yellowstone cutthroat trout retained strong populations (no indication of genetic integrity) in 32 percent of the potential range of the subspecies. In northwestern Wyoming, however, 104 streams (Greybull River and North and South Forks of the Shoshone River drainages) were sampled between 1994 and 1997, and only about 24 percent supported genetically unaltered Yellowstone cutthroat trout (Kruse et al. 2000). Based on genetic samples (6,483 km) and professional opinion (no record of stocking or presence of contaminating species; 2,966 km), May et al. (2007) estimated that up to 28 percent (assuming no introgression in all areas where professional opinion suggested no hybridization) of the historical range of Yellowstone cutthroat trout (7,945 km) still supported populations that were genetically unaltered. Occupancy is lowest in habitats near the fringe of the historical range, especially the Snake River downstream of the Portneuf River, the middle Yellowstone River, and lower Bighorn River systems (May et al. 2007). Interestingly, most populations occupy less than 16 km of stream (May et al. 2007).

Introgression appears to vary within and among watersheds. In 1990-2000, 77 stream sites from southeastern Idaho were re-examined after almost 20 years (originally sampled in the 1980's). The number of sites that contained rainbow trout x cutthroat trout hybrids rose from 23 to 37 (from 30 to 48 percent of the total sites); however, it appeared that most of the changes occurred in the Blackfoot River and two tributaries in the South Fork Snake River (Meyer et al. 2003a). At the 60 remaining sites, the number with rainbow trout and hybrids increased by only a single site (from 21 to 22 sites; Meyer et al. 2003a).

Population declines and extirpations of Yellowstone cutthroat trout have been greatest in larger, low-elevation streams where anthropogenic activities, including agriculture, livestock grazing, and resource extraction, are common, and where abundant access encouraged angler harvest and non-indigenous species introductions (Gresswell 1995, Thurow et al.1997). Remoteness of portions of the native range may have contributed to the preservation of remaining populations, and in much of this area, public lands (e.g., parks and reserves) provide increased habitat protection (Varley and Gresswell 1988). In fact, these factors may be directly related to the present occurrence of robust, genetically unaltered populations. About 65 percent of stream kilometers currently occupied by Yellowstone cutthroat trout occur on federal or Tribal government lands, and 28 percent are being managed as national parks or federally designated wilderness (May et al. 2007). Although location in these areas undoubtedly reduces that probability of anthropogenic perturbations, negative consequences of the illegal introduction of lake trout in Yellowstone Lake (Koel et al. 2005) and continuing increases in the occurrence of genetic introgression with rainbow trout suggest that location alone will not guarantee persistence of genetically unaltered populations of the Yellowstone cutthroat trout.

### Population trend

Several new studies provide updated information concerning population trends of Yellowstone cutthroat trout in its historical range. The Yellowstone Cutthroat Interagency Coordination Group summarized many of these studies in its most recent status update (May et al. 2007). This summary was based on data provided by individual state, tribal, and federal biologists who were responsible for verifying those data. Distribution and genetic status information for fluvial and lacustrine populations were included in the update (May et al. 2007).

Numerous studies document more specific trend information. For example, for almost 20 years following the original samples of 77 stream sites from southeastern Idaho, relative abundance and size structure remained quite consistent (Meyer et al. 2003a). During this period, the number of sites with introgressed populations rose, but most of those changes occurred in 17 sites in the Blackfoot River and two tributaries in the South Fork Snake River (Meyer et al. 2003a). Recent unpublished information suggests that Yellowstone cutthroat trout are currently present at 47 percent of 961 sites in the historical range of Idaho, Utah, and Nevada (84 percent of the sample sites were randomly selected). Moreover, the subspecies is the most widely distributed taxa among the sites (Meyer et al. 2006b). Of 420 sites where Yellowstone cutthroat trout were found, 341 (81 percent) currently have genetically unaltered populations. According to the most recent status assessment, Yellowstone cutthroat trout occupy 3,253 km of stream in Idaho, representing about 30 percent of historically occupied streams (10,354 km) in the state and approximately 27 percent of the current range of the subspecies (May et al. 2007).

In Montana, introgression with non-indigenous fish species and introduction of novel diseases appear to be two of the primary threats to Yellowstone cutthroat trout (Shepard and Snyder 2005). In 2005, Yellowstone cutthroat trout occupied about 2,250 km in the state, and between 2001 and 2005, there was a net decrease of only 5 km (≈ 0.2 percent; Shepard and Snyder 2005). In contrast, many fluvial populations have been reclassified from genetically unaltered (<1 percent introgression detected) or hybridized (1 to 25 percent introgression) populations to mixed-stock populations (>25 percent introgression). Some of these changes reflect data corrections rather than expansion of introgressed populations. Genetically unaltered populations (tested) are currently limited to 706 km in Montana, but potentially unaltered (no stocking records or contaminating species present) populations occur in 263 km (Shepard and Snyder 2005). Of 6,873 km historically occupied by Yellowstone cutthroat trout in Montana, about 31 percent (2,142 km) is currently occupied; this equates to about 18 percent of the current range of the subspecies (May et al. 2007).

Population trends in Wyoming were evaluated for the recent update of the 2001 range-wide status review of the Yellowstone cutthroat trout (May et al. 2007). Conversion to a 1:24,000 hydrographic coverage revealed about 320 km of currently occupied streams in Wyoming that were not previously displayed on the 1:100,000 hydrographic coverage used for the 2001 assessment (Wyoming Game and Fish Department 2005, May et al. 2007). Furthermore, based on stream survey data collected since 2001 (Wyoming Game and Fish Department 2005), it appears that the genetically unaltered Yellowstone cutthroat trout occupy an additional 491 km of historical habitat. Historically, Yellowstone cutthroat trout occupied about 10,800 km of stream in Wyoming, representing 38 percent of the total historically occupied. Currently, the subspecies occupies about 6,515 km of stream (60 percent of historical) in Wyoming, or about 54 percent of the range of the subspecies. The total currently occupied (genetically unaltered) historical habitat in Wyoming (excluding Yellowstone National Park) is now estimated to be 2,880 km (29 percent of the historical range in the state; Wyoming Game and Fish Department 2005). The primary reasons for these changes are related to the use of the 1:24,000 hydrological coverage, the revised protocol and database, and the availability of new information (field surveys and genetic tests; May et al. 2007).

In USFS Region 2, Yellowstone cutthroat trout occur in portions of the Shoshone and Bighorn national forests. According to the 2006 status update (May et al. 2007), the subspecies currently is found in about 48 percent (3,495 km) of historical stream habitat in the Upper Yellowstone Geographical Management Unit, but only 135 km of occupied stream (Clarks Fork Yellowstone River watershed) flow through lands administered by the Region (May et al. 2007). Yellowstone cutthroat trout inhabit about 26 percent

(1,772 km) of historically occupied stream in the Big Horn Geographical Management Unit, and Region 2 has management responsibility for about 833 km of stream in this unit (May et al. 2007).

Although evidence suggests that no fluvial populations of Yellowstone cutthroat trout have been extirpated from Yellowstone National Park, hybridization with introduced rainbow trout has reduced the area occupied by genetically unaltered populations (Suzanne Lewis, Superintendent, Yellowstone National Park, letter dated October 26, 2005). According to updated estimates, unaltered Yellowstone cutthroat trout currently occupy about 65 percent (851 km) of historical stream habitat in Yellowstone National Park (1,310 km) (Wyoming Game and Fish Department 2005). This estimate represents approximately 12 percent of currently occupied (genetically unaltered) stream habitat in the historical range of the subspecies. Gresswell and Liss (1995) reported that about 91 percent of the occupied range of genetically unaltered Yellowstone cutthroat trout was in Yellowstone National Park; however, recent, more precise estimates suggest that statement is incorrect. The statement more accurately represents the proportion of lake habitat in the historical range (38,500 ha) occupied by genetically unaltered Yellowstone cutthroat trout in the park (i.e., ≈ 35,000 ha in Yellowstone Lake and Heart Lake alone or about 91 percent of the historical range). In many locations within the park, including the upper Lamar River and upper Snake River drainages, populations may be relatively secure.

Genetically unaltered Yellowstone cutthroat trout continue to inhabit Yellowstone Lake, but the abundance of individuals in the lake has fluctuated substantially during the historical period. Despite NPS policies that provide substantial habitat protection from pollution and land-use practices that often degrade salmonid habitats, the native trout were subjected to the effects of non-indigenous fish introductions, spawn-taking operations, commercial fishing, and intensive sportfishing harvest through the middle part of the 20th century (Gresswell and Varley 1988, Gresswell et al. 1994). By the mid-1980's, however, it appeared that the assemblage of Yellowstone cutthroat trout in Yellowstone Lake was relatively secure (Gresswell et al. 1994).

Since the early 1990's, the introduction of non-indigenous lake trout, invasion by the parasite *Myxobolus cerebralis* (the causative agent of whirling disease), and many years of below-average precipitation in the Yellowstone Lake drainage (six of nine years between 1996-2005; WRCC 2006, http://www.wrcc.dri.edu/) have resulted in serious new declines in Yellowstone cutthroat trout abundance (Koel et al. 2005). Angler landing rates for Yellowstone cutthroat trout have declined from 2.0 fish per hour in 1994 to 0.8 fish per hour in 2004 (Koel et al. 2005). Monitoring programs that target fish ascending tributaries to spawn and annual fall gillnetting assessments provide further evidence of substantial downward trends. For example, the number of Yellowstone cutthroat trout entering Clear Creek during the annual spawning migration dropped from an average of 43,580 between 1977 and 1992 (Gresswell et al. 1994) to 3,828 between 2001 and 2004 (Koel et al. 2005). The number of spawners in 2006 was the lowest recorded in the 60-year period of record (471; Koel et al. 2007). In Pelican Creek, the second largest tributary to the lake, the number of Yellowstone cutthroat trout spawners averaged almost 24,300 between 1980 and 1983. The weir is no longer operational in Pelican Creek; however, recent sampling with nets at the historical weir site suggests that Yellowstone cutthroat trout from the lake may no longer enter the tributary (Koel et al. 2005). Similar declines in the abundance of spawners have been noted in smaller tributaries in the northwestern portion of the lake (Koel et al. 2005). The annual fall gillnetting assessment in Yellowstone Lake also reflects a decline in abundance. An average of 15.9 cutthroat trout per net was caught in 1994, but by 2002, estimates had declined to only 6.1 cutthroat trout per net (Koel et al. 2005). Reductions averaged 11 percent per year between 1994 (the year lake trout were first discovered in Yellowstone Lake) and 2002.

### Activity pattern and movements

Fish frequently move when local environmental conditions are not compatible with requirements of the individual for survival, growth, and reproduction. Salmonids, in particular, display movements that range from the local scale (e.g., microhabitats in streams and lakes) to the landscape scale (e.g., reproductive migrations that extend thousands of kilometers; Northcote 1997). Movements of potamodromous fishes, such as the Yellowstone cutthroat trout, occur in freshwater (Gresswell 1997, Northcote 1997). Although information about movement for the subspecies is available, most studies have focused on migratory behavior associated with reproduction (see **Breeding biology**).

In addition to reproductive migrations, salmonids may seasonally move to feeding or refuge habitats (Northcote 1997). For instance, movement to winter refugia has been well documented (Cunjak and Power 1986, Brown and Mackay 1995, Brown 1999). Such movements have been reported for cutthroat trout (Schmetterling 2001, Zurstadt and Stephan 2004, Colyer et al. 2005), but relatively few studies have specifically examined the Yellowstone subspecies. In the Snake River near Jackson, Wyoming (mean annual discharge = 107 $m^3$/sec), Harper and Farag (2004) reported movements to winter refugia by finespotted Snake River cutthroat trout during the winter. As water temperature declined below 1.0 °C, radiotagged-individuals moved out of deep habitats and into off-channel pools with groundwater influence.

In headwater streams where true migrations may not occur, movement is less well documented (Gresswell 1995, Northcote 1997). Recent research, however, suggests that movement (migratory and nonmigratory) of cutthroat trout is common in headwater streams (Young et al. 1997, Peterson and Fausch 2003a, Gresswell and Hendricks 2007) during a variety of seasons (Young 1996, Hilderbrand and Kershner 2000a, Lindstrom and Hubert 2004). In the broadest sense, Yellowstone cutthroat trout have the capacity for a variety of movement behaviors that are concordant with the local environmental conditions for the individual, population, and community (sensu Warren and Liss 1980, Thorpe 1994, Turchin 1998).

## Habitat

Yellowstone cutthroat trout occupy a diversity of habitats. Lacustrine populations are found in waters ranging from the size of small beaver ponds to large lakes (e.g., Yellowstone Lake, 35,400 ha; Varley and Gresswell 1988). Fluvial populations were historically common in large rivers such as the Snake River above Shoshone Falls, Idaho (mean annual discharge = 156 $m^3$/sec) and the Yellowstone River near Livingston, Montana (mean annual discharge = 107 $m^3$/sec; Clancy 1988). Many of these large-river populations have declined or disappeared. Nevertheless, Yellowstone cutthroat trout are still abundant in many small headwater streams (May et al. 2007).

In headwater basins, gradient (channel slope), elevation, stream length, and barriers to upstream dispersal influence the distribution of Yellowstone cutthroat trout at the landscape scale (Kruse et al. 1997). Using data collected at 151 sites in 56 perennial watersheds in the Greybull-Wood River drainage (northwestern Wyoming), Kruse et al. (1997) classified the presence or absence of Yellowstone cutthroat trout correctly in 83 percent of the sites using gradient alone. Adding stream length and elevation to the predictive model increased correct classification rates to 87 percent. No wild Yellowstone cutthroat trout populations were found above barriers to migration (Kruse et al. 1997). In the Salt River basin (Idaho-Wyoming), cutthroat trout densities are elevated in high-gradient reaches with a diversity of pools, riffles, and runs where brook trout (*Salvelinus fontinalis*) and brown trout (*S. trutta*) densities are low (Quist and Hubert 2005).

At the reach scale, Isaak and Hubert (2000) reported that if sampling was conducted so that the effects of confounding factors were eliminated, stream slope exhibited no significant effect on trout biomass or species composition. Similarly, stream slope did not affect areal trout density; however, when trout density was expressed volumetrically (controlling for differences in channel cross sections among reaches of different slope classes), the highest densities of trout were observed in medium-slope reaches. High-slope reaches yielded intermediate densities, and densities were lowest in low-slope reaches (Isaak and Hubert 2000).

Currently, Yellowstone cutthroat trout are often found in cold, harsh environments. Water temperatures between 4.5 and 15.5 °C are common for areas occupied by the subspecies (Carlander 1969). Maximum "scope for activity" (difference between maximum and minimum metabolic rates) in experiments conducted by Dwyer and Kramer (1975) on cultured cutthroat trout (age 1+) occurred at 15 °C. Mean daily water temperature in 11 watersheds from southeastern Idaho for July and August ranged from 6.8 to 12.9 °C (Meyer et al. 2003b). Isaak and Hubert (2004) reported that population response (density and biomass) of Yellowstone cutthroat trout to mean summer (July and August) stream temperature at 57 sites in the Salt River watershed (Wyoming) was best represented by symmetric, nonlinear curves. Peaks in curves for allopatric cutthroat trout populations occurred near 12 °C; predicted $x$-intercepts were near 3 °C and 21 °C. Some populations of Yellowstone cutthroat trout exist in streams in Yellowstone National Park with summer maxima between 5 and 8 °C (Jones et al. 1979), and isolated populations in alpine and subalpine streams overwinter with low temperatures and extreme ice conditions for up to 8 months (Varley and Gresswell 1988). Yellowstone cutthroat trout collected beneath 1 m of ice in Yellowstone Lake appeared to be actively feeding in water 0 to 4 °C (Jones et al. 1979).

In large rivers, habitat complexity may be critical for overwinter survival. For instance, the finespotted Snake River cutthroat trout in the Snake River near Jackson, Wyoming use deep run habitats most frequently during ice-free periods (Harper and Farag 2004); however, when mean water temperature is <1.0 °C, adult and juvenile cutthroat trout move to off-channel pools with groundwater influence. Although these habitats were used frequently under low-temperature conditions, they were not common in the study area (Harper and Farag 2004). Harper and Farag (2004) suggested that the multi-dimensional characteristics of the off-channel pools with groundwater influence (e.g., water depth, temperature, cover, and habitat stability) were important during cold conditions.

In the South Fork Snake River (mean annual discharge = 189 $m^3$/sec; U.S. Geological Survey 1991), Yellowstone cutthroat trout are sympatric with brown trout, and age-0 individuals of both species remain concealed at water depths <0.5 m during February through April (Griffith and Smith 1993). Griffith and Smith (1993) reported that cutthroat trout were abundant in boulder substrates but could not be found in rounded cobble; few trout of either species were found where cobble and boulders were embedded in fine sediments. Individuals of both species emerged from concealment at night and moved into the water column (Griffith and Smith 1993). In a dam-regulated portion of the Shoshone River, where native finespotted Snake River cutthroat trout are stocked annually, Dare et al. (2002) reported that the cutthroat trout and introduced brown trout both used deep pools more frequently than would be expected by availability, but both species were found most frequently in run habitats. Large boulders were commonly used as cover in both habitat types (Dare et al. 2002).

At the upper temperature extreme, Varley and Gresswell (1988) reported that water temperatures in portions of the historical range exceeded 26 °C. Currently, no large-river, warm-water populations have been documented; however, several populations occur in geothermally-heated streams in Yellowstone National Park. Yellowstone cutthroat trout apparently survive in these streams with ambient water temperature of 27 °C by finding thermal refugia (Varley and Gresswell 1988); however, Schrank et al. (2003) suggest that heat shock proteins may contribute to the survival of trout during brief periods of excessively high water temperature. In contrast, Kelly (1993) suggested that summer water temperatures exceeding 22 °C excluded cutthroat trout from Alum Creek, a tributary to the Yellowstone River in Yellowstone National Park.

Chemical conditions vary substantially across the range of Yellowstone cutthroat trout. For example, the subspecies has been collected from waters in Yellowstone National Park with total dissolved solids ranging from about 10 to 700 mg/L (Varley and Gresswell 1988), and Meyer et al. (2003b) collected Yellowstone cutthroat trout from southeastern Idaho streams with conductivities between 183 and 652 µs/cm. Although alkalinity is relatively low (mean = 64 mg $CaCO_3$/L) in areas where Yellowstone cutthroat trout occur in Yellowstone National Park, the subspecies is found in waters of the upper Snake River basin that exceed 150 mg $CaCO_3$/L alkalinity (Thurow et al. 1988). Mean alkalinity ranged from 46 to 378 mg $CaCO_3$/L for three tributaries used by fluvial-adfluvial spawners from the Yellowstone River in Montana (Byorth 1990).

Yellowstone cutthroat trout have been collected from waters with a broad range of pH (5.6-10.0+), but acidic waters (pH <5.0) are limiting (Varley and Gresswell 1988). Woodward et al. (1989) reported that cutthroat trout are sensitive to even a brief reduction in pH. For example, Kelly (1993) reported widely fluctuating pH resulting from poor buffering capacity precluded survival of Yellowstone cutthroat trout in three tributaries to the Yellowstone River in Hayden Valley (Yellowstone National Park). In contrast, Hayden (1967) reported that pH varied from 8.2 to 8.8 in four tributaries to the Snake River between Jackson Lake and Palisades Reservoir; total dissolved solids ranged from 134 to 258 mg/L.

Less has been documented concerning habitat of lacustrine populations of Yellowstone cutthroat trout. Prior to the discovery of lake trout in Yellowstone Lake (1994), most juvenile cutthroat trout (< age 3) occupied pelagic areas (Gresswell and Varley 1988), and mature Yellowstone cutthroat trout are found in the littoral zone of Yellowstone Lake (Gresswell and Varley 1988). The vast size of the pelagic area appeared to provide protection from predation by avian piscivores and larger cutthroat trout. Gresswell and Varley (1988) assumed the low proportion of juvenile Yellowstone cutthroat trout in the angler catch was associated with pelagic residence. In contrast, mature cutthroat trout travel along the shoreline to tributaries during spawning migrations, and these individuals may be particularly vulnerable to angler harvest. This relationship with pelagic habitat evolved in a system where piscivorous fish were uncommon, however, and the effects of introduced lake trout on current patterns of juvenile distribution in the lake have not been investigated.

### Food habits

Yellowstone cutthroat trout appear to be opportunistic feeders that consume food items according to availability (Thurow et al. 1988). Although diet studies for Yellowstone cutthroat trout are uncommon, trout in streams generally feed on drift, benthic invertebrates, and other fish (Allan 1995). Research suggests a strong terrestrial influence on drift in some headwater streams where there is a tight linkage with adjacent riparian areas (Romero et al. 2005). Reduced light inputs resulting from the dense riparian canopy often result in low primary productivity and a detritus-based community structure (Richardson and Danehy 2007).

Behnke (1992) suggested that Yellowstone cutthroat trout are generally more piscivorous than westslope cutthroat trout, but there is little evidence of fish consumption by the Yellowstone subspecies. One definite anomaly occurs in Heart Lake (Snake River drainage, Yellowstone National Park) where Yellowstone cutthroat trout evolved with seven other fishes (Gresswell 1995). Skinner (1985) noted an increase in growth as migratory populations of Yellowstone cutthroat trout in Idaho shifted from insectivory to piscivory. Macroinvertebrates are the primary food of mature Yellowstone cutthroat trout in Henrys Lake (Idaho) and Yellowstone Lake, however, and piscivory is rare (Benson 1961, Jones et al. 1990). For example, prior to the discovery of lake trout in Yellowstone Lake, juvenile Yellowstone cutthroat trout in the pelagic zone fed primarily on zooplankton (Benson 1961). In contrast, mature Yellowstone cutthroat trout were found in the littoral zone throughout the year, feeding on zooplankton, larger crustaceans, and aquatic insects (Benson 1961, Gresswell and Varley 1988, Jones et al. 1990). Although native longnose dace (*Rhinichthys cataractae*) and introduced populations of redside shiner (*Richardsonius balteatus*), lake chub (*Couesius plumbeus*), and longnose sucker (*Catostomus catostomus*) also occupy the littoral areas of the lake, piscivory by Yellowstone cutthroat trout was historically uncommon (Benson 1961, Jones et al. 1990).

### Breeding biology

Yellowstone cutthroat trout spawn exclusively in fluvial environments and homing is common. Homing can be defined as the return of animals to a previously occupied site instead of going to other equally probable places (Gerking 1959), and with fish, the term is most often related to migrations associated with reproduction. Natal homing (return of adult spawners to the area of their birth) by Yellowstone cutthroat trout spawners is believed to influence life-history diversity through reproductive isolation (Gresswell et al. 1994), and this behavior has been documented in many tributaries to Yellowstone Lake (Ball 1955, Cope 1957a). Repeat homing behavior (individual spawners returning to the same tributary in successive years; McCleave (1967) has been observed for fluvial spawners in the Yellowstone River (Montana; De Rito 2005); lacustrine-adfluvial spawners ascending tributaries to Yellowstone Lake (Cope 1957a, Gresswell et al. 1994, Gresswell et al. 1997a); and fluvial-adfluvial spawners in the Yellowstone River in Montana (Clancy 1988) and the Blackfoot and South Fork Snake rivers in Idaho (Thurow et al. 1988, Henderson et al. 2000). In-season homing was demonstrated in tributaries to Yellowstone Lake when individuals returned to a spawning area after experimental relocation (McCleave 1967, Jahn 1969, LaBar 1971).

Varley and Gresswell (1988) described four migratory-spawning patterns for Yellowstone cutthroat trout:

(1) Fluvial populations generally spawn within their home range in lotic systems. Migration may occur, but fluvial spawners do not enter tributary streams. After emergence, fry may move either upstream or downstream or remain near the redd (Varley and Gresswell 1988). In larger rivers, it appears that fluvial spawners may co-occur with individuals that exhibit fluvial-adfluvial migration pattern (Henderson et al. 2000, De Rito 2005). Furthermore, Yellowstone cutthroat trout spawning in the Yellowstone River between Yellowstone Lake and the Upper Falls of the river (28 km) appear to be a mixture of fluvial spawners from the river and allacustrine spawners from Yellowstone Lake (Ball and Cope 1961, Kelly 1993, Kaeding and Boltz 2001).

(2) Fluvial-adfluvial populations migrate from streams into tributaries to spawn. This pattern has been documented in the Yellowstone River in Montana (Clancy 1988, Byorth 1990, De Rito 2005), several drainages in the Snake River in Idaho (Thurow et al. 1988, Henderson et al. 2000), and in the Yellowstone River (below the Lower Falls) and Lamar River in Yellowstone National Park (Varley and Gresswell 1988). Juveniles may emigrate as fry or spend 1 to 3 years in natal tributaries before returning to the mainstem (Thurow et al. 1988, Varley and Gresswell 1988).

(3) Lacustrine-adfluvial populations live in lakes and ascend tributaries to spawn (e.g., Gresswell et al. 1994, Gresswell et al. 1997a). Although juveniles from most tributaries to Yellowstone Lake migrate to the lake shortly after emergence, some may remain in their natal stream for one or more years if the habitat is suitable (Varley and Gresswell 1988). Returns of marked fish suggested long-term (more than 2 years) lotic residency for some Yellowstone cutthroat trout that were spawned in Pelican Creek, a tributary of Yellowstone Lake (Gresswell et al. 1994).

(4) Allacustrine populations migrate from lakes downstream into the outlet stream during spawning. This spawning pattern is less common, but it has been documented in Yellowstone Lake (Ball and Cope 1961, Kaeding and Boltz 2001), Heart Lake (Varley and Gresswell 1988), and Pocket Lake (U.S. Fish and Wildlife Service, unpublished data) in Yellowstone National Park. Fry are believed to move upstream to the lake after emergence, and this behavior appears to be heritable (Raleigh and Chapman 1971, Bowler 1975).

Straying during the spawning migration is not great. For example, between 1949 and 1955, 97 percent of 244 tagged adult Yellowstone cutthroat trout that spawned more than once were collected in the Yellowstone Lake tributary where they were originally tagged (Cope 1957a). In another study conducted in 1950 and 1951, 16 to 25 percent of immature cutthroat trout emigrants tagged in Arnica Creek later returned to spawn in Arnica Creek, and none were recovered in five other monitored tributaries (Ball 1955). About 23 percent of 42,229 cutthroat trout marked at Clear Creek in 1979 returned to spawn again, and only 1 percent of the marked fish were collected in two other streams that were being monitored during that period (Jones et al. 1985). Similarly, only 10 of 333 Yellowstone cutthroat trout (3.0 percent) tagged in tributaries to the Blackfoot River failed to return to the stream in which they were marked, and all but one of these strays were found in streams that entered the Blackfoot River approximately 400 m apart (Thurow 1982). De Rito (2005) monitored six Yellowstone cutthroat trout (implanted with transmitters) for 2 years in the Yellowstone River (Montana), and the only individual that spawned in consecutive years returned to the same area to spawn during the second year. In an area of the Yellowstone River below Yellowstone Lake where Yellowstone cutthroat trout of both lake and river origin spawn annually, Kaeding and Boltz (2001) identified one putative river fish (fluvial spawner) in two consecutive years, and this individual returned to the same area in the river during both years. Only one of five putative lake fish (allacustrine) returned to the same area in consecutive years (Kaeding and Boltz 2001).

In areas where Yellowstone cutthroat trout move from lakes or large rivers to ascend tributaries to spawn, they generally return to the prespawning habitat soon after spawning is completed (Varley and Gresswell 1988). Larger prespawning habitats are believed to provide growth and refuge advantages not found in the smaller tributary systems, but in some large tributaries and the Yellowstone River below the lake, residency following spawning might extend into the fall (Gresswell 1995, Kaeding and Boltz 2001, Koel et al. 2005). Although sample sizes were small, Kaeding and Boltz (2001) hypothesized that very few Yellowstone cutthroat trout resided in the river below the lake throughout the year, and they found no evidence of reproductive isolation (spatial or temporal) between lake and river fish. Preliminary data from the Yellowstone River above Yellowstone Lake suggest a similar pattern in that area (Koel et al. 2004).

Where longevity is sufficient, iteroparity appears to be common for Yellowstone cutthroat trout (Clancy 1988, Thurow et al. 1988, Varley and Gresswell 1988), but angler harvest can affect the proportion of repeat spawners. For example, during the 1950's when angler harvest was high (200,000 to 400,000 trout annually; Gresswell and Varley 1988), Ball and Cope (1961) estimated that first-time spawners comprised up to 99 percent of spawning migrations in Yellowstone Lake. After reductions in angler harvest in the early 1970's, >20 percent of marked Yellowstone cutthroat trout were repeat spawners at Clear Creek between 1980 and 1984 (Jones et al. 1985). Up to 15 percent of Yellowstone cutthroat trout in some fluvial and fluvial-adfluvial migrations in Idaho had spawned previously (Thurow et al. 1988), and most (93 percent) repeat spawners were females (Thurow 1982).

Repeat spawning is probably related to growth, parasitic infection, and other physiological factors (Ball and Cope 1961), and alternate-year spawning appears to be more common in iteroparous populations at higher elevations (Varley and Gresswell 1988). Although iteroparity may occur in either consecutive or alternate years (Thurow et al. 1988, Varley and Gresswell 1988), Bulkley (1961) concluded that consecutive-year spawners were more common in tributaries to Yellowstone Lake. Following the reduction in angler harvest, mark-recapture studies at Clear Creek suggested that spawners returned most frequently in alternate years (Jones et al. 1985). During the 1980's, consecutive-year spawners in the Yellowstone River between Corwin Springs and Springdale (Montana) consistently exhibited slowest growth (Clancy 1988).

Spawning streams are most commonly perennial with groundwater and snow-fed water sources. Gradient of spawning areas is usually below 3 percent (Varley and Gresswell 1988), but non-migratory fluvial populations have been documented in streams with a mean gradient of 6 percent (Meyer et al. 2003b). Yellowstone cutthroat trout were not present at any of 151 locations in northwestern Wyoming when gradient was ≥ 10 percent or elevation was >3,182 m (Kruse et al.1997).

Varley and Gresswell (1988) reported that the use of intermittent streams for spawning is not well documented; however, spawning has been observed in intermittent tributaries to Yellowstone Lake. In these streams, spawning occurs during spring runoff, and fry emigrate in July and August, before late-summer desiccation. Although many fry and some adults may become stranded as discharge drops, spawning in intermittent streams may provide reproductive advantage over non-indigenous fall-spawning salmonids introduced throughout the range of the Yellowstone cutthroat trout (Varley and Gresswell 1988).

Yellowstone cutthroat trout generally spawn between March and August as water temperatures approach 5 °C (Kiefling 1978, Varley and Gresswell 1988, De Rito 2005), and at the local watershed scale, latitude, altitude, water temperature, and hydrographic relationships affect timing of migration (Varley and Gresswell 1988, Henderson et al. 2000, Meyer et al. 2003b). Although earlier studies suggested temporal separation between allacustrine and fluvial migrations into the Yellowstone River below Yellowstone Lake (Ball and Cope 1961, Kelly 1993), recent information suggests that both groups are moving into spawning areas at similar times (Kaeding and Boltz 2001). Within a year, spawner abundance generally increases as water temperature rises and discharge decreases from spring runoff peak (Varley and Gresswell 1988, Byorth 1990, Thurow and King 1994), and therefore, spawning may occur earlier at lower elevation sites. Although some Yellowstone cutthroat trout spawners enter tributaries before major increases in discharge, most fish migrate after discharge declines from the spring peak (Ball and Cope 1961, Thurow and King 1994, Gresswell et al. 1997a). Daily upstream migrations generally reach a maximum in concordance with increasing water temperature and decreasing discharge, usually between 1300-1700 hours (Byorth 1990, Jones et al. 1990).

Differences in migration timing in tributaries of the Yellowstone Lake reflect physical characteristics of the individual watersheds (Gresswell et al. 1994, Gresswell et al. 1997a). Gresswell et al. (1997a) reported that approximately two-thirds of the variation in the timing of the peak of the annual cutthroat trout spawning migrations and average length of spawners was related to mean aspect and basin area. The influence of basin-scale physical variables on date of the migration peak appeared to be manifested through the annual pattern of stream discharge. Differences among tributaries in spawner length were more difficult to explain solely in relation to stream characteristics; however, a strong relationship was observed between size structure and growth patterns of Yellowstone cutthroat trout and the physical and limnological characteristics of the lake subbasins where they were captured. Apparently, spawners were ascending streams close to the area of the lake residence (Gresswell et al. 1997a).

Although Cope (1956) observed that Yellowstone cutthroat trout spawners migrated into Arnica Creek primarily at night, angler harvest and spawn-taking operations occurring in the 1950's may have affected these results. From the 1970's through the early 1990's, most migration in tributaries to Yellowstone Lake occurred during daylight hours (Varley and Gresswell 1988, U.S. Fish and Wildlife Service unpublished data, U.S. National Park Service unpublished data). In tributaries to the Blackfoot River (Idaho), Yellowstone cutthroat trout have been observed migrating throughout the day and night, but when water temperature increases as discharge decreases, movement occurs primarily during the day (Thurow 1982). About 79 percent of adfluvial Yellowstone cutthroat trout spawners in Cedar Creek (Montana) were captured between 1400 and 1700 hours; water temperatures ranged from 12 to 14 °C during that period (Byorth 1990). In other salmonid species, nocturnal migration of spawners is uncommon (Carlander 1969).

Older and larger Yellowstone cutthroat trout are the first to migrate into tributaries to Yellowstone Lake (Ball and Cope 1961, Jones et al. 1990), and older and larger individuals move farther upstream (Cope 1957b, Dean and Varley 1974). Similar behavior has been noted with other fishes (Briggs 1955). Age, length, weight, and condition factors decline as the spawning migration progresses (Jones et al. 1990).

Although Yellowstone cutthroat trout spawners remain in tributaries to Yellowstone Lake from six to 25 days (Varley and Gresswell 1988), in some larger tributaries, such as Pelican Creek, lacustrine-adfluvial spawners may remain for many months (Gresswell et al. 1994). Furthermore, it appears that allacustrine Yellowstone cutthroat trout from Yellowstone Lake may remain in the Yellowstone River below the lake throughout the summer (Schill and Griffith 1984, Kaeding and Boltz 2001). Males usually migrate into spawning tributaries earlier than females and remain in spawning streams longer (Ball and Cope 1961). Often during the initial portion of spawning migrations, some individuals move into and out of tributaries repeatedly before spawning (U.S. Fish and Wildlife Service, unpublished data). Nocturnal emigration of postspawners is common prior to peak discharge, but as the run progresses, movement usually occurs during the day (Varley and Gresswell 1988).

Optimum temperature for spawning is between 5.5 and 15.5 °C (Varley and Gresswell 1988), but water temperatures in spawning areas are generally >10 °C. For example, Byorth (1990) found that 77 percent of Yellowstone cutthroat trout spawners in Cedar Creek ascended when water temperatures were 12 to 14 °C. For 13 years between 1977 and 1992, maximum daily water temperature in Clear Creek, a tributary to Yellowstone Lake, ranged between 10 and 14.2 °C on the date of peak spawning migration (U.S. Fish and Wildlife Service, unpublished data). In a tributary to the South Fork Snake River (Idaho), Thurow and King (1994) reported that maximum daily water temperature ranged from 16 to 20 °C during the Yellowstone cutthroat trout spawning migration. Mean water temperature in 11 streams across the range of Yellowstone cutthroat trout in Idaho was 10.4 to 16.1 °C during the spawning and incubation period (June-August; Meyer et al. 2003b).

Optimum size for gravel in Yellowstone cutthroat trout spawning areas is 12 to 85 mm in diameter (Varley and Gresswell 1988). In 11 redds from Cedar Creek (Montana), Byorth (1990) estimated approximately 74 percent (by weight) gravel (2 to 63.5 mm in diameter) and 17 percent cobble (63.5 to 256 mm in diameter). Substrate was less than 100 mm in diameter in a Snake River (Idaho) tributary, and approximately 60 percent of the substrate was in the 16- to 64-mm size-class, 15 percent was in the 6.4- to 16-mm size-class, and 20 percent was less than 6.4 mm in diameter (Thurow and King 1994).

Although Varley and Gresswell (1988) suggested that Yellowstone cutthroat trout spawn wherever they find optimum temperature and substrate, other factors determine use in specific localities. Research in tributaries to Yellowstone Lake suggested that spawners were not always associated with areas with the greatest concentration of spawning gravel, and forest cover did not affect the distribution of redds (Cope 1957b). Yellowstone cutthroat trout entering tributaries early in the spawning migration often move upstream farther than individuals arriving later in the migration (Cope 1957b, Dean et al. 1975). Thurow and King (1994) noted that severe drought conditions influenced the selection of spawning sites of Yellowstone cutthroat trout spawners in consecutive years, and physical cues, such as water velocity and water depth, may be critical for locating redds in areas with a high probability of hatching success and fry survival. Kiefling (1978) suggested that discharge volume and movement of fine sediments limited spawning in the Snake River mainstem between Jackson Lake Dam and Palisades Reservoir, and only 10 of 36 tributaries (28 percent) have been reported to have a high potential for recruitment (Hayden 1967). Springs are the common feature of the productive spawning tributaries in that part of the watershed (Kiefling 1978).

In a tributary to the South Fork Snake River (Idaho), water depth at Yellowstone cutthroat trout spawning sites varied from 9 to 55 cm deep, but more than 80 percent of the redds occurred in water 10 to 30 cm deep (Thurow and King 1994). Average water depth was 20 cm beside the pit and 21 cm upstream from the pit. In a smaller tributary of the Yellowstone River (Montana), Byorth (1990) reported that redds were constructed at a mean depth of approximately 12 cm during a 2 year study period (Byorth 1990).

Thurow and King (1994) measured water velocities of 16 to 73 cm/sec within 5 cm of completed Yellowstone cutthroat trout redds, and the mean was 42 cm/sec beside the redd and 46 cm/sec upstream from the redd. Mean velocity near redds in two tributaries to the Yellowstone River (Montana) was approximately 24 cm/sec and 38 cm/sec, respectively (Byorth 1990). In one stream, velocities ranged from 0 to 68 cm/sec, but velocities of 16 to 27 cm/sec were recorded near the redds. Water velocity was more variable (14 to 71 cm/sec) near redds in the second stream (Byorth 1990).

Mean redd size (n = 66) in the South Fork Snake River tributary was 1.58 m long by 0.60 m wide; redds covered an area of approximately 1 $m^2$ (Thurow and King 1994). Superimposition of redds generally occurred laterally or immediately downstream of existing redds. This phenomenon occurs commonly in spawning streams (Mills 1966, Byorth 1990), but Thurow and King (1994) suggested that redd superimposition occurring laterally or downstream of the tailspill may not disturb the eggs because eggs are often deposited in the center of the upstream edge of the tailspill.

Yellowstone cutthroat trout fry generally seek areas of low velocity in streams (Varley and Gresswell 1988). For example, Byorth (1990) reported that water velocities were 3 and 5 cm/sec for two tributaries of the Yellowstone River, and almost 50 percent of Yellowstone cutthroat trout fry were captured where velocities were <2 cm/sec. Fry occurred in areas where mean depth was approximately 11 cm (range = 3-24 cm; Byorth 1990). Byorth (1990) hypothesized that differences in stream substrate at sites used by Yellowstone cutthroat trout fry probably reflected variation in available substrate materials in the two streams.

### Demography

Although Yellowstone cutthroat populations are broadly distributed and many remain robust in headwater streams, migratory populations in large rivers and lakes have declined substantially (Meyer et al. 2006b, May et al. 2007). Headwater populations frequently occur above migration barriers that protect them from competition, predation, and introgression from non-indigenous trout, and many of these populations are believed to be large enough to be resilient to stochastic disturbance (Kruse et al. 2001, Meyer et al. 2006b, May et al. 2007). In large rivers and lakes, however, the threat of interspecific interactions with non-indigenous trout is substantial (Kruse et al. 2000, Meyer et al. 2006b), and there is a high probability of continued decline (Kruse et al. 2000). These conditions suggest a significant departure from historical demographic conditions where large interconnected assemblages of Yellowstone cutthroat trout thrived throughout their historical range (Kruse et al. 2000). Seemingly conflicting management strategies focused on reconnecting fragmented habitats and isolating genetically unaltered populations each have potential demographic ramifications that may limit the geographical extent of persistent assemblages of the subspecies (Hilderbrand and Kershner 2000b, Kruse et al. 2001, Peterson et al. 2008).

#### *Genetic characteristics and concerns*

Allozyme data suggest that the Yellowstone cutthroat trout underwent a geologically recent genetic bottleneck during the Pleistocene glaciation. For example, Loudenslager and Gall (1980) reported that in a survey of 10 Yellowstone cutthroat trout populations over a broad geographical range, only 8 percent of the genetic diversity was due to divergence among populations. Furthermore, Yellowstone cutthroat trout exhibited the lowest among-population genetic divergence of eight potamodromous salmonids examined by Allendorf and Leary (1988). Subsequent examination of genetic structure of cutthroat trout in Yellowstone Lake using protein electrophoresis and mitochondrial DNA (mtDNA) failed to detect genetic differences among spawning populations (Shiozawa and Williams 1992).

In a recent study, Cegelski et al. (2006) used data from six polymorphic microsatellite loci to investigate genetic diversity and population structure of Yellowstone cutthroat trout in Idaho and Nevada. Yellowstone cutthroat trout were genetically structured at the major river drainage level, but evidence suggested that habitat fragmentation had altered that structure (Cegelski et al. 2006). For example, the system with the least altered migration corridors (11 major river drainages examined in the study) exhibited the highest levels of genetic diversity and low levels of genetic differentiation. High levels of genetic differentiation were observed at similar or smaller geographic scales in stream networks that have been more altered by anthropogenic activities (Cegelski et al. 2006).

Another recent study using microsatellite loci failed to find significant genetic differentiation among spawning populations from Yellowstone Lake using traditional statistical methods and Bayesian clustering analysis, but nested clade analysis yielded statistically significant evidence for restricted gene flow among populations (Janetski 2006). Apparently, there is some degree of reproductive isolation despite ongoing gene flow. These results may provide some insight into observed phenotypic variation among spawning populations in tributaries to the lake (Gresswell et al.1994, Gresswell et al. 1997).

The taxonomic status of finespotted cutthroat trout in the Snake River is complex. The largespotted form of the Yellowstone cutthroat trout was historically found throughout the range of the subspecies (Varley and Gresswell 1988, Behnke 1992). In contrast, the finespotted form was limited to the Snake River drainage, and Behnke (1992) speculated that it was the dominant form in the Snake River from Jackson Lake downstream to Palisades Reservoir. The two forms are currently found in the same stream networks in the Snake River basin, but they are usually not found in the same habitat (Novak et al. 2005). Furthermore, it appears that the largespotted form is common in the headwaters and many of the tributaries of the Snake River (Novak et al. 2005).

The two forms are difficult to distinguish genetically (Loudenslager and Kitchin 1979, Loudenslager and Gall 1980); however, the two spotting patterns appear to be heritable (Behnke 1992). Recent studies using mitochondrial DNA and six microsatellite loci failed to find genetic differences between forms, but there were genetic differences among drainages (Novak et al. 2005). One of two distinct haplotype clades was found throughout the Snake River watershed above Palisades Dam, but members of this clade were most common in the Jackson Hole area and in the Gros Ventre River. The second common clade was found more frequently in the Hoback River, Snake River Canyon, and Greys River.

Efforts to identify genetically unaltered populations of Yellowstone cutthroat trout are an integral part of current management of the subspecies throughout their range. The importance of this effort has been formalized in the Memorandum of Understanding among Montana Fish, Wildlife, and Parks; Idaho Department of Fish and Game; Wyoming Game and Fish Department; Nevada Division of Wildlife; Utah Division of Wildlife Resources; Yellowstone National Park; Grand Teton National Park; and the USFS (Anonymous 2000). In the Yellowstone River drainage, both in Yellowstone National Park and outside the Park in Montana, genetic sampling has been pursued vigorously in recent years. Most management agencies require positive genetic identification prior to protecting populations of Yellowstone cutthroat trout, and therefore, this work is critical to the persistence of the subspecies (Varley and Gresswell 1988). Concomitantly, protecting and genetically restoring introgressed populations of Yellowstone cutthroat trout where genetic purity is ≤ 98 percent may be warranted in some cases (Anonymous 2000, May et al. 2007).

In an attempt to maintain genetic integrity of indigenous populations of the Yellowstone subspecies, stocking programs have been modified in Montana, Idaho, and Wyoming. Management of fluvial fisheries in Montana emphasizes wild trout populations, and stocking in lotic systems was terminated in 1974 (Vincent 1987). In Idaho and Wyoming, stocking in the upper Snake River basin is restricted to waters that do not support viable populations of genetically unaltered Yellowstone cutthroat trout, and in areas statewide where stream stocking still occurs, the only rainbow trout that have been sterilized through heat or pressure treatment are released (IDFG 2007b). Because of widespread stocking of the finespotted Snake River ecotype of Yellowstone cutthroat trout in Wyoming, the current distribution of this form has been extended into many portions of the Yellowstone River drainage where they were not present historically (May et al. 2007).

The use of piscicides to remove undesirable fishes has a long history in the United States (Meronek et al. 1996), but employing this technique to protect indigenous species from hybridization and competition with other salmonid species was infrequent until the 1980's (Rinne and Turner 1991, Finlayson et al. 2005). In Colorado, Wyoming, and Montana, piscicides have been successfully used to protect and reestablish indigenous cutthroat trout subspecies (Gresswell 1991, Harig et al. 2000). In some cases, removing non-indigenous salmonids using electrofishing has been attempted in order to avoid some of the drawbacks associated with the use of piscicides (Thompson and Rahel 1996, Kulp and Moore 2000); however, success has been mixed (Finlayson et al. 2005, Meyer et al. 2006a). Although removal of non-indigenous species may be critical for the protection and reintroduction of Yellowstone cutthroat trout in some areas, it is extremely expensive and difficult to achieve long-term success (Meronek et al. 1996, Finlayson et al. 2005).

*Life history characteristics*

Mean age of spawners varies across the range of the Yellowstone subspecies. Individuals in most fluvial populations from the upper Snake River in Idaho mature at age 4 or 5, but variation occurs among populations (Thurow et al. 1988). In Henrys Lake, Yellowstone cutthroat trout mature at age 3 (Thurow et al. 1988). Age at maturity has also been estimated to be age 3 in the Yellowstone River between Corwin Springs and Springdale, Montana (Clancy 1988). Where longevity of fish in a population is greater, such as Yellowstone Lake (Gresswell et al. 1994), mean age for lacustrine-adfluvial spawners approached 6 years during the 1980's (Gresswell et al. 1997a).

Average size of Yellowstone cutthroat trout spawners is also variable. Thurow et al. (1988) reported that mean total length (TL) of Yellowstone cutthroat trout spawners in Idaho varied between 300 and 500 mm. Few fish less than 200 mm TL were mature, and most fluvial-adfluvial spawners were ≥ 275 mm. In the Yellowstone River in Montana, Clancy (1988) classified fish >300 mm as adults, and spawners from two tributaries to the river varied from 322 to 368 mm TL in 1988 and 1989 (Byorth 1990). Benson and Bulkley

(1963) reported that fish above 300 mm TL were mature in Yellowstone Lake, and most fish less than 250 mm were immature. Data collected between 1985 and 1992 suggested that mean TL of Yellowstone cutthroat trout spawners in tributaries to Yellowstone Lake ranged from 305 to 405 mm (Gresswell et al. 1997a). In small subalpine lakes and streams where there are few migratory spawners, Yellowstone cutthroat trout may mature between 100 and 130 mm.

A recent study of 610 Yellowstone cutthroat trout from 11 streams and rivers in southeastern Idaho revealed a strong relationship between length and age at sexual maturity and physical characteristics of the drainage (Meyer et al. 2003b). Length-at-maturity models were more informative than age-at-maturity models. Length at maturity was positively correlated to stream order and channel width, and negatively correlated to gradient; there were weak associations with conductivity, elevation, mean aspect, and mean summer water temperature. Furthermore, length at maturity was generally greater for migratory populations than local fluvial (nonmigratory) populations. For example, individuals from the South Fork Snake River matured at 300 mm TL and 5 years of age. In other migratory and local populations, maturity began at ages 2 to 3 and lengths of 100 to 150 mm. At sites with nonmigratory life histories, most 100 to 250 mm Yellowstone cutthroat trout were mature (Meyer et al. 2003b).

Angler harvest can directly affect age and length of Yellowstone cutthroat trout spawners (Gresswell and Varley 1988, Gresswell et al. 1994). During the mid-1960's when landing rate (number of fish/hour) and mean length of captured fish were declining in Yellowstone Lake, mean age of Yellowstone cutthroat trout at Clear Creek declined to 3.9 years. Following implementation of restrictive regulations in the early 1970's, the average age in the spawning run has increased to 5.8 years (Gresswell et al. 1994). After catch-and-release (no harvest) regulations began on the Yellowstone River below Yellowstone Lake in 1973, the mean age of spawners increased from 3.7 years in 1974 to 6.1 years by 1986 (Gresswell 1995).

Restrictive angling regulations can also affect mean length of fish as exploitation is reduced. For example, following implementation of restrictions for Yellowstone Lake between 1969 and 1975, length of spawners at Clear Creek increased from a mean of 365 mm (mid-1960's) to 399 mm by 1988 (Gresswell 1995). On the Yellowstone River below the lake, mean length of spawners increased from 362 mm in 1974 (1 year following the catch-and-release regulation) to 402 mm in 1991 (Gresswell 1995). The proportion of Yellowstone cutthroat trout >330 mm increased after catch-and-release regulations were enacted on the Yellowstone River in Montana (Shepard 1992).

Male:female ratio varies among sites. For example, Thurow et al. (1988) reported that except for the migration to the Henrys Lake Hatchery, females were more abundant than males in fluvial-adfluvial spawning populations sampled in Idaho. Females were also more abundant in lacustrine-adfluvial spawning migrations in tributaries to Yellowstone Lake (Gresswell et al. 1997a). Males often dominated the early portion of spawning migrations, however, and the proportion of females increased as the spawning migration progressed (U.S. Fish and Wildlife Service, unpublished data). Between 1945 and 1953, mean male: female ratios for six tributaries ranged from 0.61:1 to 0.74:1 (Ball and Cope 1961). Estimates for 13 sample years between 1973 and 1992 at Clear Creek ranged from 0.52:1 to 0.75:1 (U.S. Fish and Wildlife Service, unpublished data).

In a recent study of Yellowstone cutthroat trout populations at 11 sites in southeastern Idaho (Meyer et al. 2003b), male:female ratios varied from 0.52:1 to 2.70:1 (n = 29-80), and males were more common than females at eight sites (Meyer et al. 2003b). In this study, a single sample was collected from a 200 to 400-m section at each site. Byorth (1990) and Berg (1975) found that males were more common early in the spawning migration, but as the migration peaked, the male:female ratio approached 1:1.

Although demographic factors affect male:female ratios observed at different sites, sample size, time of year, and location of the sample site (within a stream) can confound estimates. Furthermore, it is apparent that angler harvest may affect male:female ratio. For example, for the first two years after angling regulations were changed to catch-and-release (no harvest) on the Yellowstone River below Yellowstone Lake, male: female ratios were 0.73:1 and 0.79:1, however, after two years male:female ratios dropped below 1.06:1 only three times (1982, 1986, and 1989). These estimates were based on weekly synoptic samples collected throughout the spawning migration, sample sizes were large, and methods remained unchanged through the 18-year period (Jones et al. 1992).

Mean fecundity of Yellowstone cutthroat trout varies among populations. For example, estimates in the early 1980's were 1,393 eggs/female for Clear Creek (Yellowstone Lake; mean length = 394 mm) and 1,577 (mean length = 319 mm) and 2,930 eggs (mean length = 518 mm) for females from Henrys Lake (Thurow et al. 1988). Mean fecundity of females collected from the South Fork Snake River (mean length = 377 mm) during that period was 1,413 eggs (Moore and Schill 1984). Furthermore, Cope (1957a) reported that the relationship between egg size and ovary weight differed significantly among spawning females from three tributaries to Yellowstone Lake.

Population fecundity (total number of eggs deposited by females in a population; Bagenal 1978) is influenced by the total number of female spawners and the population structure (mean length and age of females). For example, relative fecundity (number of eggs/kg of female body weight; Bagenal 1978) at Clear Creek was similar from the 1950's through the early 1990's (approximately 2,600 eggs/kg), but average fecundity of individual female Yellowstone cutthroat trout rose with increases in mean length during that period. As the number of spawners increased between 1975 and 1992 in response to changes in angling regulations, population fecundity rose from about 6.2 million eggs (1950's) to an average of almost 32 million eggs (Gresswell 1995).

Estimates of instream mortality of Yellowstone cutthroat trout spawners have varied considerably among studies; however, the relative influence of monitoring procedures and fluctuations in predation by grizzly bears (*Ursus arctos*) and American white pelicans (*Pelecanus erythrorhynchos*) has not been investigated in detail. Based on returns of recaptured fish (originally tagged with Petersen disc tags) to five tributaries of Yellowstone Lake between 1949 and 1953, Ball and Cope (1961) reported that average instream mortality of cutthroat trout spawners was 48 percent. In Arnica Creek during 1951 and 1952, 28 percent of Yellowstone cutthroat trout spawners died near spawning sites, and an additional 1 percent died before postspawning emigration was complete (Welsh 1952). The mean estimate of instream mortality based on total counts of upstream and downstream migrants for five sample years at Clear Creek (1977-1979, 1983, and 1984) was 13 percent (Jones et al. 1985). Instream mortality at Clear Creek increased from 1987 to 1992 (mean = 31 percent; U.S. Fish and Wildlife Service, unpublished data).

In redds located in three tributaries to Yellowstone Lake, egg mortality of Yellowstone cutthroat trout was estimated to range between 12 and 42 percent (Mills 1966), and mortality was inversely related to water flow through gravel. Previous studies by Ball and Cope (1961) suggested that egg mortality might be as high as 60 to 70 percent. Roberts and White (1992) demonstrated that angler wading may reduce survival under experimental conditions, but under natural conditions, mortality of eggs and fry associated with wading does not appear to be significant (Kelly 1993).

Eggs generally hatch in 25 to 49 days (310 Celsius temperature units, sum of mean daily temperatures above 0 °C). Larvae emerge from the gravel about 2 weeks later (Ball and Cope 1961, Mills 1966, Kelly 1993) and move to shallow areas with low discharge. Emigration of individuals from migratory parents occurs soon afterwards in most tributaries to Yellowstone Lake (Varley and Gresswell 1988). Although young-of-the-year Yellowstone cutthroat trout are locally numerous in the Yellowstone River below Yellowstone Lake, fish <250 mm are not common (Schill and Griffith 1984, Kelly 1993). Kelly (1993) reported that numbers of young-of-the-year fish declined more than 90 percent within 25 days after peak emergence.

In southeastern Idaho, fry of migratory parents often move downstream shortly after emergence (Thurow et al.1988), but in some tributaries, juvenile Yellowstone cutthroat trout may not emigrate for 1 to 3 years. Similar patterns have been reported for tributaries to Yellowstone Lake (Benson 1960, Gresswell et al. 1997a) and the Yellowstone River drainage in Montana (Byorth 1990). Distance from redd to stream mouth may influence the length of time that fry remained in tributaries to Yellowstone Lake (Welsh 1952), and substantial numbers may remain over winter in some streams (Gresswell et al. 1994). There is some evidence of density-dependent downstream migration related to habitat availability (Thurow et al.1988).

## Community ecology

### *Sympatric species*

Following the Pleistocene glaciation, rainbow trout replaced the Yellowstone cutthroat trout in most of the Columbia River Basin below Shoshone Falls on the Snake River (Behnke 1992). The falls were formed about 14,500 years ago (Oviatt et al. 1992) during a cataclysmic flood from Lake Bonneville, a late Pleistocene lake. Since that time, Yellowstone cutthroat trout have evolved sympatrically with 10 other fish species also occurring above Shoshone Falls (Thurow et al. 1988). Seven of these fishes historically occurred with Yellowstone cutthroat trout in the Heart Lake drainage of the upper Snake River in Yellowstone National Park (Jordan 1891, Smith and

Kendall 1921, Dean and Varley 1974). On the east side of the continental divide, the longnose dace and the Yellowstone cutthroat trout were sympatric above the Upper Falls of the Yellowstone River (Benson and Bulkley 1963). Below the falls, Yellowstone cutthroat trout co-occurred with mountain whitefish (*Prosopium williamsoni*), mottled sculpin (*Cottus bairdi*), longnose sucker, white sucker (*Catostomus commersonii*), and longnose dace (Clancy 1988).

### *Predation*

There are many natural predators in the range of the Yellowstone cutthroat trout, but most of the available information pertains to the Yellowstone Lake ecosystem. For example, in the Yellowstone Lake watershed alone, 42 bird and mammal species use fish for food, including bald eagles (*Haliaeetus leucocephalus*) and grizzly bears (Schullery and Varley 1995). Prior to the illegal introduction of lake trout to Yellowstone Lake, piscivorous avifauna probably had the greatest effect on cutthroat trout in that drainage (Gresswell 1995, Stapp and Hayward 2002a). The size and biomass of fish consumed per day varied among 20 or more bird species using this resource (Swenson 1978, Swenson et al. 1986, Schullery and Varley 1995), but the total biomass of cutthroat trout consumed by piscivorous avifauna may have exceeded 100,000 kg annually (Davenport 1974, Gresswell 1995).

Ward (1922) suggested that American white pelicans alone removed 350,000 Yellowstone cutthroat trout (approximately 105,900 kg) annually during the 1920's (based on population estimates of 500 to 600 pelicans). Although recent evidence implies that this estimate was excessive, Davenport (1974) found that biomass of Yellowstone cutthroat trout consumed by white pelicans was at least 34,500 kg (400 pelicans) and 16,800 kg (195 pelicans) for 1973 and 1974, respectively. She concluded that interannual variation in consumption was related to fluctuation in reproductive success on the pelican rookery in the southern part of the lake (Davenport 1974). Pelicans were common on the Yellowstone River below Yellowstone Lake in the early 1990's, and Kaeding (2002) reported that discharge and the number of redds in the major spawning areas on the river contributed substantially to interannual variation in the number of pelicans observed in the river.

During the breeding season (April-August), up to 23 percent of the diet of bald eagles in the Yellowstone Lake area consisted of Yellowstone cutthroat trout between 1972 and 1982 (Swenson et al. 1986), and during the peak spawning period in Yellowstone Lake (May-July, Ball and Cope 1961; Gresswell et al. 1997a), eagles consumed Yellowstone cutthroat trout almost exclusively. In the Snake River and major tributaries from the mouth of Lewis Lake to mouth of Henrys Fork, cutthroat trout comprised about 8 percent of the diet during the same period (Swenson et al. 1986).

Other piscivorous birds include osprey (*Pandion haliaetus*), great blue heron (*Ardea herodias*), common merganser (*Mergus merganser*), California gull (*Larus californicus*), common loon (*Gavia immer*), Caspian tern (*Hydroprogne caspia*), Barrow's goldeneye (*Bucephala islandica*), bufflehead (*B. albeola*), belted kingfisher (*Megaceryle alcyon*), and double-crested cormorant (*Phalacrocorax auritus*). All of these birds breed in the Yellowstone Lake area and depend on the abundant food source provided by cutthroat trout spawners and larval offspring. With the possible exception of the cormorant, these birds primarily focus on fish in shallow portions of the littoral area and tributaries where Yellowstone cutthroat trout are the common (Schullery and Varley 1995, McEneaney 2002).

Model predictions suggest that historically mammalian predators consumed about 7 percent of the Yellowstone cutthroat trout population in Yellowstone Lake annually (Stapp and Hayward 2002a). Cutthroat trout are especially vulnerable to predation during the spawning period, and they have been documented to be seasonally important in the diet of grizzly bears in the lake area (Mealey 1980, Mattson and Reinhart 1995, Haroldson et al. 2005). Because dumps had become the primary feeding areas for bears by the 1960's, it was hypothesized that the bears had to relearn fishing behavior after the dumps were closed in 1970 (Reinhart and Mattson 1990). Management actions that reduced angler harvest of Yellowstone cutthroat trout in the 1970's may have had indirect positive effects on grizzly bears, and the number of streams frequented by bears increased from 1974-75 to 1985-87 (Reinhart and Mattson 1990). Following the introduction of lake trout, however, numbers of spawning Yellowstone cutthroat trout and indices of bear use declined on streams near the developments of Grant Village and Lake during 1990-95 (Reinhart et al. 2001). More recently, Haroldson et al. (2005) documented lakewide declines in the number of cutthroat trout spawners between 1989 and 2000.

In the Yellowstone Lake area, river otter (*Lontra canadensis*) are believed to depend on Yellowstone cutthroat trout throughout the year (Crait and Ben-David 2006). During the summer, cutthroat trout are the primary prey consumed near the spawning tributaries and the lake itself. Crait (2002) recently documented that otters influence the prevalence and growth of plants by transferring lake-derived nutrients into the riparian area. Although river otters also consume longnose suckers from the lake, they appear to be a minor component of the otter diet, and Crait and Ben-David (2006) suggest that this is a direct reflection of the relative abundance of the two species in Yellowstone Lake.

Perhaps the most significant effect of predation on the Yellowstone cutthroat trout has occurred in Yellowstone Lake since the illegal introduction of lake trout. Cutthroat trout in the lake evolved without large piscine predators (Gresswell 1995), and there is no evidence of adaptive behaviors to reduce predation. Based on information collected from 1996 through 1999, Ruzycki et al. (2003) reported that lake trout commonly consumed cutthroat trout from 27 to 33 percent of their body length, and an average of 41 cutthroat trout annually by the introduced predator. Given sustained removal of lake trout at 1999 levels, the population in 2002 was predicted to be about 3,500 individuals (Ruzycki et al. 2003); however, the removal of lake trout by NPS biologists exceeded 12,000 lake trout in that year (Bigelow et al. 2003). Removals increased to more than 70,000 in 2007 alone (P. Bigelow, personal communication, 2008).

Since lake trout were first discovered in 1994, the annual spawning migration of Yellowstone cutthroat trout into Yellowstone Lake tributaries has declined precipitously (Koel et al. 2005), and relative abundance estimates from annual monitoring with gill nets are at the lowest point since the program began in 1969 (Gresswell et al. 1994). These declines in Yellowstone cutthroat abundance may substantially affect other predators throughout the Yellowstone Lake ecosystem (Varley and Schullery 1995, Stapp and Hayward 2002a, Crait and Ben-David 2006). For example, pelicans have maintained the breeding colony in the Southeast Arm of Yellowstone Lake, but large numbers are now foraging on the Yellowstone River 80 km north of Yellowstone National Park and on the Madison River west of Bozeman, Montana (R.E. Gresswell, unpublished data). Indices of grizzly bear use on monitored spawning streams have decreased (Haroldson et al. 2005), and estimates of Yellowstone cutthroat trout consumption by bears (2,226 trout annually, Felicetti et al. 2004) are <2 percent of estimates of trout consumed by lake trout in the 1990's (Ruzycki et al. 2003, Felicetti et al. 2004).

No published accounts were located that documented predation of Yellowstone cutthroat trout in other parts of the historical range, but it is assumed that cutthroat trout are important to avian and terrestrial predators wherever population abundance is sufficient. Predation by non-indigenous salmonids (e.g., brook trout and brown trout) is often suggested as a mechanism for the population extirpation for all subspecies of cutthroat trout, but direct evidence is scarce. It is assumed that the effects of piscine predation observed in Yellowstone Lake are severe because prior to the introduction of lake trout, predation by fish was low (Gresswell 1995, Ruzycki et al. 2003). In contrast, it appears that cutthroat trout in Jackson Lake (Grand Teton National Park) and Heart Lake (Yellowstone National Park) historically preyed on other fishes with which they evolved, and therefore, the effects of introduced lake trout on the native assemblage may not have been as extreme.

### *Competition*

Competition is often suggested as a regulating factor influencing salmonid population abundance, but direct competition is difficult to document (Larkin 1956). This is especially evident in studies of competition between salmonid and non-salmonid fishes. For example, there was no evidence that the introduction of longnose sucker, redside shiner, and lake chub into Yellowstone Lake had negative effects on the Yellowstone cutthroat trout population (Gresswell and Varley 1988). Although Marrin and Erman (1982) reported competition between brown trout and rainbow trout in Stampede Reservoir (California), neither tui chub (*Gila bicolor*) nor Tahoe sucker (*Catostomus tahoensis*) appeared to be competing with either salmonid species. Spatial and temporal niche separation may reduce competition in this example, and in general, interspecific competition would be greatest between species with similar niche requirements (Marrin and Erman 1982).

Competition among salmonids has been studied frequently, but the majority of studies have focused on individual-level interactions, rather than population-level responses (Peterson and Fausch 2003a). Furthermore, the outcome varies. In the headwaters of the Madison River, westslope cutthroat trout and fluvial Arctic grayling (*Thymallus arcticus*) were extirpated following the introduction of non-indigenous brown trout and rainbow trout (Jones et al. 1981); however, the specific roles of competition, predation, and angler harvest were difficult to differentiate. In contrast, Yellowstone cutthroat trout have persisted in sections of the Yellowstone River (Montana) where brown trout and brook trout have become established (Clancy 1988). In fact, brown trout more frequently co-occur with Yellowstone cutthroat trout than westslope cutthroat trout in Montana (Wang and White 1994). In some Idaho streams, Yellowstone cutthroat trout persist in areas with introduced brown trout and brook trout, if habitat has not been degraded and angler harvest is minimal (Thurow et al. 1988).

These observations suggest that the outcome of competitive interactions among fishes is context-specific and therefore can be affected by abiotic conditions such as water temperature (Fausch 1989, Shepard 2004). Dunson and Travis (1991) designated such outcomes as condition-specific competition. For example, in experiments under warm water conditions (19 to 22 °C), Reeves et al. (1987) reported that production of steelhead in the presence of redside shiner declined by 54 percent compared to estimates when shiners were absent. In streams, however, steelhead occupied similar habitats when shiners were present or absent (Reeves et al. 1987). Similar results have been documented for interactions between salmonids such as rainbow trout and brook trout (Cunjak and Green 1986) and Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) and brook trout (De Staso and Rahel 1994, Peterson et al. 2004).

Cutthroat trout may be less likely to coexist with brook trout than other non-indigenous salmonids (Griffith 1988), and in Yellowstone National Park, Yellowstone cutthroat trout have been extirpated from most areas where brook trout have been introduced (Varley and Gresswell 1988). Among the mechanisms for displacement, competitive exclusion has probably been cited most frequently, and niche overlap may be greater between Yellowstone cutthroat trout and brook trout than with either of these fishes and other salmonid species (Gresswell 1995). Alternatively, species replacement (Griffith 1988, Shepard 2004) may explain the extirpation of Yellowstone cutthroat trout in some cases. Yellowstone cutthroat trout are easily captured by anglers (Schill et al. 1986, Thurow et al. 1988, Varley and Gresswell 1988), and brook trout are less vulnerable to angling than cutthroat trout (MacPhee 1966). Differential mortality associated with angler harvest could eventually lead to dominance of the least susceptible group. Once another salmonid has replaced cutthroat trout, the situation is often irreversible.

Peterson et al. (2004) documented that although brook trout invasion does not always result in complete extirpation of cutthroat trout throughout watersheds, this non-indigenous invader is effective in headwater streams of the central Rocky Mountains. Apparently, brook trout can recruit and survive as well or better than native greenback and Colorado River cutthroat trout, immigrate rapidly, and ultimately replace the native cutthroat through suppression of vulnerable juvenile life stages (Peterson et al. 2004). Peterson et al. (2004) suggested that brook trout depress cutthroat trout at mid-elevation sites through age-specific biotic interactions that reduce survival of juveniles, but water temperature limits reproduction of cutthroat trout at colder high-elevation sites. Recent findings by Coleman and Fausch (2007a) suggest that these two cutthroat trout subspecies are reproductively limited in streams where <900 degree-days accumulated during the summer. Apparently, a recruitment bottleneck occurs 4 to 6 weeks following swim-up; it is associated with temperature-related energy deficits (Coleman and Fausch 2007b).

There is some evidence that disturbance can influence species interactions (Roelke et al. 2003), and Dunham et al. (2003) suggested that watershed response to fire may facilitate replacement by non-indigenous species. Although few studies have directly addressed this hypothesis, in a recent study from the Bitterroot River basin (Montana), Sestrich (2005) found that where connectivity in stream networks was high, westslope cutthroat trout and bull trout (*Salvelinus confluentus*) populations were not extirpated following disturbance. In fact, these native fishes recovered more quickly than brook trout in most watersheds.

Peterson and Fausch (2003a) proposed that biotic interactions, causing reduction in reproductive rates or survival at particular life stages, net emigration, disease (either debilitating or fatal) introduced by the invader, or some combination of these factors, represent the only direct mechanisms by which the abundance of the native species can decline following invasion by non-indigenous fish. Additionally, abundance of the invading species must increase through reproduction, high survival, net immigration, or a combination of these factors (Peterson and Fausch 2003a). Furthermore, it appears that biotic interactions negatively affect native cutthroat trout even when habitat factors are favorable (Quist and Hubert 2005). Although recent modeling by Hilderbrand (2003) provides additional support for these conclusions, it is apparent that habitat degradation and loss of connectivity can directly affect the vital rates identified above.

*Disease and parasites*

Prior to the late 1980's, enzootic levels of disease in naturally reproducing populations of Yellowstone cutthroat trout were poorly documented. The causative agent for furunculosis (*Aeromonas salmonicida*) had been isolated from spawners in the Yellowstone River below Yellowstone Lake (U.S. Fish and Wildlife Service, unpublished data), and MacConnell and Peterson (1992) reported the occurrence of the proliferative kidney disease (PKD) in a feral population of cutthroat trout in a remote reservoir in Montana. Since that time, whirling disease, caused by the exotic parasite *Myxobolus cerebralis* has been found in the native range of the Yellowstone cutthroat trout (Burckhardt et al. 2002), and negative population-scale effects have been documented in some areas (Koel et al. 2006). For example, whirling disease is believed to have caused the virtual extirpation of spawning Yellowstone cutthroat trout ascending Pelican Creek from Yellowstone Lake (Koel et al. 2005). This tributary once supported thousands of spawning cutthroat trout from the lake (Gresswell et al. 1994). Interestingly, nonmigratory (fluvial) Yellowstone cutthroat trout are still prevalent in the headwaters of Pelican Creek despite high densities of *M. cerebralis* (J. Alexander, unpublished data).

The life cycle of *Myxobolus cerebralis* includes two intermediate spore stages (triactinomyxons and myxospores) and two obligate hosts (the oligochaete *Tubifex tubifex* and various salmonid fish species) (Wolf et al. 1986). A substantial amount of information has emerged in the last decade on the species, sex, and age differences in susceptibility of the fish host (e.g., Hedrick et al. 1999, Ryce et al. 2005), effects of water temperature on the development of *T. tubifex* and *M. cerebralis* (DuBey et al. 2005, Kerans et al. 2005a), and diagnostics (Andree et al. 1998). For example, Yellowstone cutthroat trout exhibit a strong disease response to exposure to *M. cerebralis* (Hiner and Moffitt 2001, Wagner et al. 2002, Burckhardt et al. 2002). Moreover, habitat characteristics influence infection rates, and Burckhardt et al. (2002) found that in the Salt River drainage (Wyoming), stream width, stream depth, and fine sediment deposition were positively correlated with the occurrence of whirling disease in Yellowstone cutthroat trout. Channel slope, distance to the mainstem, and site elevation were negatively correlated with infection in this study (Burckhardt et al. 2002).

There are at least 64 other parasitic species associated with cutthroat trout (Hoffman 1967, Heckmann and Ching 1987). Of these, 18 have been collected from Yellowstone Lake (Heckmann 1971, Heckmann and Ching 1987), and 55 to 60 percent of more than 10,000 fish examined from tributaries to Yellowstone Lake had parasites in the 1950's (Cope 1958). In other portions of the current range of the Yellowstone cutthroat trout, the extent of parasite occurrence in populations is not well documented (Woodbury 1934, Bangham 1951, Hoffman 1967).

The most infamous of these parasites is the tapeworm found in Yellowstone Lake. Originally identified as *Diphyllobothrium cordiceps* (Heckmann and Ching 1987), taxonomic work in the 1980's yielded two species (*D. ditremum* and *D. dendriticum*) instead of one (Otto and Heckmann 1984). The American white pelican is a definitive host of the tapeworm (Linton 1891), and there was a plan in the 1920's to destroy pelican eggs on the rookery in an effort to reduce the incidence of tapeworms by controlling the bird population (Varley and Schullery 1983). Infestation rates can be high (46 to 100 percent; Woodbury 1934, Bangham 1951, Post 1971, Heckmann and Ching 1987), but the effects on mortality have not been assessed. Although there has been speculation that stunting and diminished egg production are possible (Hall 1930), these outcomes have never been substantiated. Cutthroat trout may harbor more than 400 plerocercoids (Heckmann 1971), but activity levels appear to be unchanged in some individuals with a high level of parasitism (Post 1971).

The primary concern to anglers of high infestation is aesthetic (Linton 1891, Post 1971); however, there is some evidence that human infections are possible (Heckmann and Ching 1987). Historically anglers from Yellowstone Lake often responded by discarding parasitized fish. This was a major issue in the late 1950's when harvest limits on Yellowstone Lake were 3 fish per day, but by the late 1970's, disposal rates were very low for Yellowstone cutthroat trout under a 2-fish, 330 mm maximum-size limit. Apparently, there is a reduced infection rate in younger fish that comprise the harvest under regulations that stipulate the release of larger trout (Gresswell 1995).

Other parasites are ubiquitous. Parasitic copepods (*Lepeophtheirus salmonis*, *Lernaeopoda bicauliculata*, *Salmincola edwardsii*, and *Salmincola* sp.; Heckmann and Ching 1987) are usually located on gills, fins, and points of fin insertion, but highest infestation density is often at the point of fin insertion (Cope 1958). Leeches (*Piscicola salmositica* and *Illinobdella* sp.; Heckmann and Ching 1987) are found all over the exterior body, apparently without preference (Cope 1958).

An eye fluke *Diplostomum baeri buccelentum* occurs quite commonly in Yellowstone cutthroat trout collected from Yellowstone Lake (Heckmann and Ching 1987, Dwyer and Smith 1989). These flukes cause diplostomatosis, or eye fluke disease of fishes. The density of worms appears to be the major factor influencing the effect on visual acuity of these trout (Heckmann and Ching 1987). Severe infections may compromise an individual's ability to feed, and ultimately its growth.

Parasite infestation varies among spawning tributaries (Cope 1958). Furthermore, males are usually infested with more parasitic copepods, and females support a greater number of leeches. In general, infestation rates decrease throughout the spawning migration, and fewer downstream migrants are parasitized than upstream migrants are. The greatest incidence of leeches was during the latter portion of the migration; however, this may vary among streams and sample years (Cope 1958, Gresswell 1995).

# Conservation

## *Threats*

### Non-indigenous and invasive species

For the purposes of this report, a non-indigenous species refers to a species, such as a rainbow trout, that was deliberately introduced into an area for fishery management purposes (Winters et al. 2004b). Although these species may have replaced native fishes or in many cases, invaded new watersheds, many are important to recreational anglers (Quist and Hubert 2004). Invasive species refers to a species (e.g., *Myxobolus cerebralis*, the causative agent for whirling disease), that may have been introduced inadvertently or gained access by natural means (invaded) and has no socially or biologically redeeming value (Winters et al. 2004b).

Introduced fishes, both exotic (naturally occurring outside the North American Continent) and those arising from interbasin transfers of fishes native to North America, collectively constitute the primary threat to Yellowstone cutthroat trout resulting from non-indigenous species (Varley and Gresswell 1988, Kruse et al. 2000). In the last decade, however, invasive invertebrates, including the New Zealand mud snail (*Potamopyrgus antipodarum*) (Hall et al. 2003, Kerans et al. 2005b) and *Myxobolus cerebralis*, the causative agent of whirling disease (Bartholomew and Reno 2002), have been found in the native range of the Yellowstone cutthroat trout. As noted above, whirling disease may be directly responsible for population-scale declines of Yellowstone cutthroat trout (Koel et al. 2005); however, the New Zealand mud snail has not been linked to negative effects on populations of Yellowstone cutthroat trout (Hall et al. 2003).

Human activities have altered biodiversity significantly by adding new species to regional-scale species pools (originally related to continental movement patterns and evolutionary events) and providing the means for some species to circumvent major biogeographic filters (Rahel 2002), such as glaciation and geographic barriers, that prevent colonization of some aquatic systems. Although interbasin transfers of fish by humans have probably occurred periodically through history, major continental-scale introductions of non-indigenous fishes have increased (frequently in conjunction with official government programs) since the latter part of the 19th century (Behnke 1992, Rahel 1997). In Montana alone, 375 unauthorized introductions of fishes were documented through the mid-1990's, and 45 different species were illegally introduced into 224 different waters (Vashro 1995). Early introductions were associated with the perceived paucity of native fishes suitable for food and fishing in the western United States (Jordan 1891, Dill and Cordone 1997, Nico and Fuller 1999). In general, the pattern of introductions has proceeded from the eastern United States west; however, rainbow trout, primarily associated with coastal states in the West, have been introduced throughout the country (Nico and Fuller 1999, Rahel 2002).

Natural movement of non-indigenous fishes from areas where they have become established is common. In fact, it appears that continued immigration from optimal sites and recolonization of inadequate areas may sustain invasions where environmental conditions limit recruitment of non-indigenous competitors (Peterson and Fausch 2003a). Barriers to movement may restrict access to non-indigenous species in some cases; however, the probability of interbasin transfer, either legally or illegally, is also a significant problem. For example, lake trout were first discovered in Yellowstone Lake in 1994 (Kaeding et al. 1996). Evidence from otolith chemical composition suggests that the source was Lewis Lake (Munro et al. 2005), a roadside lake located within 30 km of Yellowstone Lake. Lake trout were first introduced to Lewis Lake in

1890 following initial surveys that suggested the lake and nearby Shoshone Lake were devoid of fish (Jordan 1891, Visscher 1984). It appears that introductions of lake trout to Yellowstone Lake occurred repeatedly since the late 1980's (Munro et al. 2005).

Once a non-indigenous species has become established in the regional species pool, it can be expected to colonize all new areas that are accessible and where it is compatible with existing abiotic conditions and biological community (Brown and Moyle 1997, Fausch et al. 1997, Rahel 2002). Although invasions from downstream (upstream directed) are common, movement from upstream (downstream directed), especially where non-indigenous are introduced to headwater lakes, may actually be more rapid because of the lack of dispersal barriers (Adams et al. 2001). Because abiotic conditions, such as those related to the hydrologic cycle, are constantly fluctuating, invasions often exhibit an "ebb and flow" pattern, especially in habitats to which invaders are poorly adapted (Larson et al. 1995, Strange and Habera 1998). In many cases, anthropogenic habitat alteration may enhance the probability of successful establishment by a non-indigenous invader. For example, eutrophication and removal of apex predators have been implicated as factors that are often associated with the non-indigenous species (Byers 2002). Similarly, the introduction of a top predator, like lake trout, into a system that has not evolved with a native predator (e.g., Yellowstone Lake), is often linked to shifts in the local biotic community (especially the native Yellowstone cutthroat trout) that can extend to the broader ecosystem (Varley and Schullery 1998, Stapp and Hayward 2002b, Ruzycki et al. 2003).

Unfortunately the outcomes of invasions are often difficult to predict because few studies have been conducted at the population scale, the important interface at which the demographics of invading species and resident (native) species interact (Peterson and Fausch 2003b). In cases where the invader can interbreed with the native fish, such as introductions of rainbow trout or other cutthroat trout subspecies into native Yellowstone cutthroat trout systems, hybridization is a frequent outcome. Mechanisms such as competition and predation have been studied at the individual level; however, abiotic factors that affect the ability of invaders to adapt can modify the outcome (Dunson and Travis 1991).

### *Hybridization*

For the Yellowstone cutthroat trout, hybridization resulting from introductions of rainbow trout and non-indigenous cutthroat trout subspecies is a ubiquitous cause of the decline and extirpation of the subspecies (Allendorf and Leary 1988, Varley and Gresswell 1988, Kruse et al. 2000). Because hybrids between rainbow trout and Yellowstone cutthroat trout are developmentally successful, progeny may appear as morphological and meristic intermediates between parental types or virtually identical to a single parental type (Ferguson et al. 1985, Bettles et al. 2005). Therefore, it is difficult to verify genetic integrity based on morphological data alone, and nuclear allozymes, mitochondrial DNA (mtDNA) haplotypes, and nuclear DNA have proven useful for detecting hybridization (Leary et al. 1987, Campbell et al. 2002, Ostberg and Rodriguez 2002).

Hybridization with rainbow trout has resulted in the disappearance of Yellowstone cutthroat trout in some Idaho rivers, such as the Henrys Fork Snake River (Griffith 1988, Van Kirk and Gamblin 2000) and portions of the Blackfoot, Portneuf, and Teton rivers (Varley and Gresswell 1988). Henderson et al. (2000) reported spatial overlap among Yellowstone cutthroat trout, rainbow trout, and hybrids in the South Fork Snake River, and hybridization was expanding. Where rainbow trout have been stocked in the historical range of Yellowstone cutthroat trout in Montana, there are hybrid populations of the two species (Hanzel 1959). Half of 16 samples from tributaries to the Yellowstone River in Montana that were analyzed by Allendorf and Leary (1988) were genetically unaltered, and because sample sites were selected without prior knowledge of genetic integrity, these findings may represent a realistic representation of hybridization in the Yellowstone River drainage (Allendorf and Leary 1988). Kruse et al. (2000) reported that only 26 percent of the 104 Wyoming trout streams still support genetically pure Yellowstone cutthroat trout, and 21 of the stream segments with genetically pure populations contained no other fish species. None of the samples from 22 streams in the Greybull River watershed yielded indications of rainbow trout introgression, but there were five streams in the South Fork Shoshone River drainage with genetically pure Yellowstone cutthroat trout. In the North Fork Shoshone River watershed, all 58 occupied streams supported populations of rainbow trout or *Oncorhynchus* hybrid swarms.

Reproductive isolation has apparently prevented hybridization between Yellowstone cutthroat trout and rainbow trout in some areas, even where physical barriers to movement are not present (Henderson et al. 2000, Kruse et al. 2000, May et al. 2007). For example, there was no evidence of hybridization between rainbow trout and Yellowstone cutthroat trout populations in four tributaries to the upper Blackfoot River (Wishard et al. 1980). Yellowstone cutthroat trout spawn in May and June in headwater reaches of these drainages, and rainbow trout of hatchery origin typically spawn from winter through spring in lower reaches of the drainage (Thurow 1982).

A recent study of 73 radio-tagged Yellowstone cutthroat trout, rainbow trout, and cutthroat x rainbow trout hybrids in the Yellowstone River (Montana) suggested that spatial distributions in the five most used spawning areas were similar; however, temporal overlap in those areas was lower (De Rito 2005). For example, rainbow trout and hybrids commonly spawned in April and May, but most were no longer in the spawning areas during June when the majority of Yellowstone cutthroat trout moved in to spawn. Furthermore, genetic samples of spawning aggregations were 97.5 to 100 percent Yellowstone cutthroat trout; rainbow trout introgression was only observed in one of the aggregations (De Rito 2005).

Unfortunately, it appears that following initial hybridization, the proportion of introgression in a population tends to increase. Henderson et al. (2000) reported that hybridization was expanding in the South Fork Snake River, and they observed substantial spatial overlap in spawning among rainbow trout, cutthroat trout, and rainbow x cutthroat hybrids. Overlap in spawning period also occurred, and it appeared that the timing of peak discharge during spring snowmelt could affect the potential for hybridization by influencing run timing (Gresswell et al. 1997a, Henderson et al. 2000). Hitt et al. (2003) observed that hybridization between rainbow trout and westslope cutthroat trout in the Flathead River system was occurring primarily with post-$F_1$ hybrids and was advancing in an upstream direction. If the mechanisms associated with hybridization are similar in the South Fork Snake River, temporal overlap might be expected to be higher among Yellowstone cutthroat trout and hybrids than with rainbow trout parent stocks (Allendorf et al. 2004).

Introduction of cutthroat trout from non-indigenous subspecies or populations is another cause of introgression of Yellowstone cutthroat trout (Allendorf and Leary 1988). Over 818 million eggs were gathered from Yellowstone Lake tributaries between 1899 and 1957 (Varley 1979), and Yellowstone cutthroat trout from Yellowstone Lake were stocked in waters from over one-half of the 50 United States, most Canadian provinces, and several other countries (Gresswell and Varley 1988, Varley and Gresswell 1988). Henrys Lake also supported a substantial egg-taking operation that resulted in a similar dispersion of Yellowstone cutthroat trout outside the native range of the subspecies (K. Meyer, personal communication, 2008). Intraspecific introgression of Yellowstone cutthroat trout with numerous other cutthroat trout subspecies resulted from these programs (Marnell et al. 1987, Gresswell 1988, Carl and Stelfox 1989). In Yellowstone Lake alone, planting hatchery-reared fry in the lake and its tributaries led to the potential mixing of up to 68 genetic entities (assuming only one type per spawning migration; Gresswell and Varley 1988).

*Competition, predation, and disease*

Although the level of threat associated with competition and predation is often difficult to evaluate, there are numerous examples of population-level declines of Yellowstone cutthroat trout following the introduction/invasion of non-indigenous fishes. Kruse et al. (2000) suggested that non-indigenous fishes were the most important reason that Yellowstone cutthroat trout declined in the Greybull River and North Fork and South Fork Shoshone River. Furthermore, there was no evidence that habitat changes had substantially influenced remaining populations (Kruse et al. 2000). Moreover, lack of habitat segregation among brook trout, rainbow trout, and cutthroat trout suggests that competition may be substantial among these salmonid fishes in the habitats that were sampled (Kruse et al. 1997). Although brown trout are often present in larger watersheds in Montana where migratory Yellowstone cutthroat trout are common, the mechanism that apparently supports sympatry has not been documented (Wang and White 1994). In the Salt River basin (Idaho–Wyoming), Quist and Hubert (2005) found that when brown trout and brook trout densities were low, cutthroat trout density was highly variable and more closely related to habitat characteristics. Cutthroat trout density was always low if brown trout and brook trout densities were high, even when habitat conditions were favorable (Quist and Hubert 2005).

The effects of direct predation of Yellowstone cutthroat trout have been documented over the past decade in Yellowstone Lake, and current evidence suggests that non-indigenous lake trout are directly linked to the observed declines of Yellowstone cutthroat trout in the lake (Ruzycki et al. 2003, Koel et al. 2005). This is especially critical because Yellowstone Lake represented what was believed to be the largest inland population of cutthroat trout in the world (Gresswell and Varley 1988). According to Ruzycki et al. (2003), cutthroat trout approximately 27 to 33 percent of the body length of lake trout are vulnerable to predation, and juvenile cutthroat trout are especially vulnerable. Effects of predation have not been studied extensively in other portions of the historical range, but lake trout, brown trout, and brook trout are all piscivorous, and predation is widely assumed to be one of the mechanisms that has allowed them to successfully replace native cutthroat trout (Kruse et al. 2000, Quist and Hubert 2005).

Although non-indigenous lake trout appear to be directly linked to the observed declines of Yellowstone cutthroat trout in Yellowstone Lake (Ruzycki et al. 2003, Koel et al. 2005), whirling disease may also contribute. Up to 20 percent of all juvenile and adult Yellowstone cutthroat trout in Yellowstone Lake are infected with *Myxobolus cerebralis* (Koel et al. 2006), but infection does not appear to be uniform throughout the watershed. For example, *M. cerebralis* has been detected in Pelican Creek, Clear Creek, and the Yellowstone River downstream from the lake, but the Yellowstone River upstream of the lake inlet and 13 other spawning tributaries have tested negative for the parasite (Koel et al. 2006). Risk of infection is highest in the Yellowstone River and Pelican Creek (Koel et al. 2006). Recent data suggest that >90 percent of the fry from Pelican Creek are infected with the parasite, and since 2001, few wild-reared fry have been observed in the lower portions of the watershed (Koel et al. 2005). In the headwaters of the stream, however, nonmigratory (fluvial) Yellowstone cutthroat trout are prevalent despite high densities of *M. cerebralis* (J. Alexander, unpublished data).

### Habitat degradation

Habitat degradation associated with surface water diversions, dam construction, grazing, mineral extraction, timber harvest, and road construction is common in lotic environments throughout the United States (Meehan 1991). In portions of the historical range of Yellowstone cutthroat trout, these activities have negatively affected this subspecies' distribution and abundance (Thurow et al. 1997, Van Kirk and Benjamin 2001, Winters et al. 2004a). Barriers to migration, reduced discharge, sediment deposition, groundwater depletion, streambank instability, erosion, increased water temperature, and pollution are all associated with human activities (Winters et al. 2004b), and these perturbations are especially prevalent in portions of the historical range that occur on non-federal lands at lower elevations.

Although there are no impoundments on the Yellowstone River in the historical range of the Yellowstone cutthroat trout, numerous impoundments in the Snake River have altered historical fish migration patterns. Reduction of peak flows, rapid fluctuation in discharges related to hydropower generation, and sediment loss immediately below dams have major effects downstream (Van Kirk and Benjamin 2001). Reduced sediment inputs and increased embeddedness limit spawning and rearing habitats below dams, and altered discharge patterns exacerbate these problems (Thurow et al. 1988, Van Kirk and Benjamin 2001). For example, spawning and rearing areas have been isolated in the Blackfoot, Portneuf, South Fork Snake, Teton, Henrys Fork Snake, and main-stem Snake rivers (Thurow et al. 1988), and reduced winter flows below a dam on the South Fork Snake River have been linked to significant mortality of age-0 Yellowstone cutthroat trout (Elle and Gamblin 1993). Van Kirk and Benjamin (2001) reported strong correlation ($r = 0.63$) between hydrologic integrity (an index of cumulative effects of reservoirs, surface water withdrawals, and consumptive water use) and the status of native salmonids (including the Yellowstone cutthroat trout) in 41 watersheds in the headwaters of the Snake River and Yellowstone River basins.

Water diversions have been identified as a significant factor in the decline of Yellowstone cutthroat trout (Hadley 1984, Thurow et al. 1988, Idaho Department of Fish and Game 2007a), and there are thousands located in the current range of the subspecies (Winters et al. 2004a, Idaho Department of Fish and Game 2007a). In many cases, spawning habitat for Yellowstone cutthroat trout in tributaries is lost where water diversion occurs annually (Byorth 1990), and in the Yellowstone River (Montana), population density of Yellowstone cutthroat trout is generally greatest in the vicinity of tributaries that support spawning migrations. Irrigation withdrawals often prohibited adfluvial migrations into Reese Creek, a tributary to the Yellowstone River on the north boundary of Yellowstone National Park, prior to water-rights adjudication (Jones et al. 1990). In Idaho, irrigation removals seriously affect the Blackfoot, Henrys Fork Snake, Portneuf, Raft, Teton, and main-stem Snake rivers and Willow Creek (Thurow et al. 1988). Degraded water quality and unscreened irrigation ditches contribute to the problems associated with water diversions throughout the range of the Yellowstone cutthroat trout (Johnson 1964, Clancy 1988, Thurow et al. 1988). In addition to decreased water availability and formation of passage barriers, water diversions provide new routes for species invasions when ditches traverse watershed boundaries (Winters et al. 2004a).

Habitat fragmentation can negatively affect Yellowstone cutthroat trout persistence by directly reducing total available habitat, inhibiting dispersal behaviors, simplifying habitat structure, and limiting resilience to stochastic disturbance. Wofford et al. (2005) reported that gene diversity and allelic richness of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in a 2,200 ha watershed were lowest in small tributaries where immigration had been blocked by culverts. Similarly, genetic diversity and genetic population structure of Yellowstone cutthroat trout from 45 sites in streams of Idaho and Nevada appeared to be naturally structured at the major river drainage scale, but structure has been altered by habitat fragmentation (Cegelski et al. 2006). Furthermore, fragmentation can destroy critical dispersal pathways among populations, preventing the repopulation following local extirpation (Guy et al. 2008). Genetic structure of coastal cutthroat trout populations in 27 watersheds isolated above barriers to fish passage was strongly affected by connectivity and watershed complexity and the influence of these habitat characteristics on reproductive isolation (Guy et al. 2008). The management significance of low genetic variability is directly linked to low population size, and regardless of hypothetical genetic effects on persistence, the probability of extirpation from random perturbations greatly increases as population abundance (genetic variability) declines (Hilderbrand and Kershner 2000b, Kruse et al. 2001).

Barriers to fish movement associated with road culverts play a major role in habitat fragmentation, and in headwater streams, genetic and demographic isolation can potentially compromise long-term population persistence (Wofford et al. 2005). Excessively high outfall drops, insufficient pools for resting below culverts, shallow water depth in culverts, and high water velocities through culverts, all interfere with fish passage (Winters et al. 2004b). Culverts that alter or totally block fish migration (Belford and Gould 1989) are ubiquitous throughout the range of the Yellowstone cutthroat trout (Winters et al. 2004b, Idaho Department of Fish and Game 2007a). In some cases where Yellowstone cutthroat trout population densities are limited by the available spawning habitat, improperly designed culverts prevent passage to tributaries (Clancy 1988, Belford and Gould 1989). Even in Yellowstone National Park, culverts on several tributaries to Yellowstone Lake reduce access to adfluvial spawners, and at least two culverts totally block annual spawning migrations (Dean and Varley 1974, Jones et al. 1986). In many portions of the current range of the Yellowstone cutthroat trout, reach/site level analysis to assess the influence of culverts and other road related issues has not been conducted (Winters et al. 2004a).

Effects of excessive livestock grazing on riparian habitats have been documented extensively (Gresswell et al. 1989, Platts 1991). In the current range of the Yellowstone cutthroat trout, the effects of grazing on contemporary distribution and abundance vary. For example, habitat degradation resulting from livestock grazing in the Yellowstone River drainage is believed to be less of a threat to indigenous populations of Yellowstone cutthroat trout than hybridization and dewatering (C. Clancy, 1995). In Idaho, however, intensive livestock grazing has caused degradation of riparian areas and subsequent stream bank sloughing, channel instability, erosion, and siltation in many drainages (Thurow et al. 1988), and alterations are broadly distributed on private and public lands throughout the upper Snake River basin in Idaho and Wyoming (Binns 1977, Thurow et al. 1988). In contrast, Kruse et al. (2000) found no evidence that habitat alteration had significantly affected the remaining populations of Yellowstone cutthroat trout in northwestern Wyoming, and non-indigenous fishes appeared to be the primary reason that populations have declined. In fact, Winters et al. (2004b) suggest that livestock grazing is only one factor affecting the condition of riparian habitats, and roads, recreational activities, wild ungulate grazing, and historical activities (e.g., tie drives) have substantial effects on current conditions.

Mineral extraction does not appear to have had broad impacts on the distribution of Yellowstone cutthroat trout, but there is some evidence of local extirpations. For example, Thurow et al. (1988) reported increased sedimentation associated with phosphate mines in the Blackfoot River drainage (Idaho). Recent research by Van Kirk and Hill (2006) suggests that selenium concentrations in trout associated with phosphate mining in southeast Idaho have the potential for negative population-level effects, but a rigorous statistical evaluation of selenium concentrations and trout populations in the area has not occurred. An abandoned gold mine in the headwaters of Soda Butte Creek (Montana, upstream from Yellowstone National Park) caused extensive changes in water quality through the 1960's (Jones et al. 1982). During that period, fish populations were depressed downstream in Yellowstone National Park, and anglers had minimal success (Arnold and Sharpe 1967). Following reclamation of the tailings, input of pollutants was reduced, and the fishery improved (Jones et al. 1982). Moreover, fish are absent from tributary reaches near abandoned tailings and mine adits located in Boulder River (Montana), but populations of brook trout, rainbow trout, and Yellowstone cutthroat trout are found further downstream (Farag et al. 2003). Elevated concentrations of Cd, Cu, and Zn were associated with increased mortality of trout at sites located near the mine (Farag et al. 2003).

### Climate change

Climate change may ultimately be the greatest threat to the persistence of Yellowstone cutthroat trout because it will exacerbate current negative effects of non-indigenous aquatic species and habitat degradation. Mean air temperatures have increased by approximately 0.6 °C globally during the past 100 years (Intergovernmental Panel on Climate Change 2001, Walther et al. 2002). There have been two primary periods of warming, between 1910 and 1945 and from 1976 to present, and warming during the latter period has occurred at a rate almost double that of the first. This rate of change represents the fastest rate of warming in last 1,000 years (Intergovernmental Panel on Climate Change 2001, Walther et al. 2002).

Air temperature is expected to continue warming globally from 1.4 to 5.8 °C during the 21$^{st}$ century (Intergovernmental Panel on Climate Change 2001). Changes in maximum summer temperatures and minimum winter temperatures will affect stream temperature the most (Keleher and Rahel 1996). With warming temperatures, the current ranges of cold-water species are expected to shift north in latitude and up in elevation. Using an upper temperature threshold of 22 °C for a guild of coldwater fish (brook trout, cutthroat trout, and brown trout) as a constraining variable, Keleher and Rahel (1996) predicted that the length of streams occupied by trout in Wyoming would decrease 7.5 to 43.3 percent for increases in temperature from 1 to 5 °C. These estimates include minor increases in suitable habitats at high elevations as temperatures increase.

Fish inhabiting lakes will also be affected. Shallow lakes may desiccate completely as temperatures increase, and water depth of deeper lakes will probably decrease. It appears that lake habitats for coldwater fish may decline up to 45 percent, and the largest negative impacts will be in lakes of moderate depth (≤ 13 m maximum depth; Stefan et al. 2001).

Most of the future climate projections have been based on models focused on temperature at the global scale, and such models do not account for the interaction of physical variables that will be affected by climate change at the regional or landscape scale. For example, Jager et al. (1999) demonstrated that hydrology is another important variable to consider with effects of climate change on trout. Changing the juxtaposition of the fish incubation period with flow-related disturbances in models revealed non-additive interactions between hydrologic and temperature effects (Jager et al. 1999).

Recently, Williams et al. (2007a) assessed the effects of three potentially detrimental factors related to climate change (i.e., warmer summer temperatures, increased winter flooding, and increased wildfires) on Bonneville, Colorado River, and westslope cutthroat trouts. The analysis identified subwatersheds and river basins where the three cutthroat trout subspecies might be at the greatest risk of extirpation. Although results varied among subspecies and subwatersheds, risk from higher stream temperatures and winter flooding was predicted to be greatest for small, isolated cutthroat populations, especially those at lower elevations (Williams et al. 2007a). Analyses of this type can be especially useful in evaluating how climate change may interact with factors that negatively influence persistence of native cutthroat trout, including the Yellowstone subspecies.

Global model predictions may be useful for preliminary understanding of climate change in aquatic systems, but the output from regional models is needed to predict effects at finer spatial scales. Furthermore, it is apparent that the complexities related to regional environmental heterogeneity further alter the watershed-scale responses to climate change. For example, recent research suggests that potential future climate conditions may have no current analog and some existing climate states may disappear completely (Williams et al. 2007b). Local land management history and species pool are other factors that should be considered as models become more complex and spatially resolved because habitat fragmentation and non-indigenous species have reduced the capacity of aquatic systems to respond to the effects of disturbances such as climate change (Ebersole et al. 1996).

Climate change may have substantial effects on the persistence of Yellowstone cutthroat trout through complex behavioral responses to the effects of temperature and precipitation and combined effects of these variables on the hydrological cycle. Changes in migration cues may decrease reproductive potential for Yellowstone cutthroat trout in allopatric situations, and when rainbow trout are present, introgression may increase (Henderson et al. 2000). In fact, the interactions among fishes that currently co-occur, or that reside in near proximity, may change dramatically under altered climate scenarios, and these interactions have not been investigated.

### Demographic effects of disturbance

Disturbances, regardless of the ultimate source (i.e., anthropogenic or natural), are commonly generalized as either pulse or press (Bender et al. 1984, Lake 2003). A pulse disturbance is a sudden, short duration change that steadily dissipates; a press disturbance begins rapidly and reaches a level that is maintained for a long period. A less commonly discussed type of disturbance (ramp disturbance) steadily increases through time and across space (Lake 2000, Lake 2003). Biological responses to any of these types of disturbance may similarly be a pulse, press, or ramp type (Angeler and Moreno 2007).

Most examples of pulse disturbance have natural sources (e.g., fire, floods, and windstorms), but some anthropogenic activities (e.g., chemical spill) may act as pulse disturbance. Press disturbance is more commonly ascribed to anthropogenic causes such as grazing, road construction, and mining. Lake (2000, 2003) used ramp disturbance to describe supra-seasonal droughts, or those droughts defined by extended declines in rainfall. This type of disturbance might be manifested in many different ways during prolonged climate change.

Although these terms are convenient for conceptualizing types of disturbance and response, most disturbance events exhibit aspects of at least two of these conceptual categories. For example, wildfires commonly exhibit both pulse and press effects, and attempts to define them are often contingent on temporal and spatial scale (Gresswell 1999). For example, large, infrequent disturbances (e.g., hurricanes, tornadoes, fires, volcanic eruptions, floods) are by definition linked to prolonged temporal interludes and large spatial expression.

Many anthropogenic activities, such as timber harvest, may also exhibit mixed characteristics (Gresswell 2005). At the local scale, effects of clear-cut logging may be similar to an extreme fire event where most of the standing biomass is removed, but at the landscape scale, the area affected (i.e., converted to an earlier successional state) over short periods is much greater. For example, about 20 percent of 4.6 million ha of forest in western Oregon were clear-cut harvested between 1972 and 1995 (Cohen et al. 2002, Gresswell 2005). It can be argued, however, that during the next several decades the area affected by large fires may become much greater, and that under extended drought conditions, the severity of these fires will continue to increase (Westerling et al. 2006).

Other anthropogenic disturbances may be classified as press disturbance. Examples include roads, mining, and point-source pollution. Roads contribute directly to disturbance in aquatic systems by changing erosion patterns, fragmenting watersheds, and negatively affecting water quality (Trombulak and Frissell 2000); each of these disturbances is immediate and long lasting. At the watershed scale, Trombulak and Frissell (2000) argued that the pattern of fragmentation associated with roads could be termed hyperfragmentation because of the interactive effects of fragmentation and habitat loss that emerge when the effects of terrestrial and aquatic disturbance related to roads are considered simultaneously.

Ramp disturbance is a useful term for describing anthropogenic activities whose effects continue to increase through time and space, such as suburban development. It may be especially appropriate for describing effects of climate change during the coming decades. Effects of increasing temperature, changing hydrological patterns, more frequent and widespread wildfires, and human development can be expected to increase negative consequences of current conditions related to the effects of habitat degradation and introduced species.

### Angler harvest

Substantial declines in population abundance have been related to overharvest of Yellowstone cutthroat trout throughout the historical range of the subspecies (Binns 1977, Hadley 1984, Gresswell and Varley 1988). Vulnerability to angling is high. In fact, in the late 1980’s individuals in the Yellowstone River (Yellowstone National Park) were captured an average of 9.7 times during the 108-day angling season, and many tagged Yellowstone cutthroat trout were captured two or three times in a single day (Schill et al. 1986). Although anglers are attracted to the fishery by high catchability, this characteristic can lead to substantial declines in abundance if restrictive regulations are not implemented (Gresswell 1995, Gresswell and Varley 1998, Gresswell and Liss 1995).

In some cases where non-indigenous salmonids are sympatric with Yellowstone cutthroat trout, angler harvest may contribute to species replacement and eventual extirpation (Griffith 1988). Because non-indigenous salmonids are usually less vulnerable to angling than Yellowstone cutthroat trout (MacPhee 1966; Schill et al. 1986; Gresswell and Liss 1995), unequal angler mortality could contribute to the eventual dominance of non-indigenous fishes. If another salmonid replaces cutthroat trout, the situation is generally irreversible (Moyle and Vondracek 1985).

All state, federal, and tribal agencies that have management authority for Yellowstone cutthroat trout currently manage the subspecies as sport fish (Wyoming Game and Fish Department 2005, Idaho Department of Fish and Game 2007a, May et al. 2007). In many cases, however, conservation or preservation of Yellowstone cutthroat trout is the primary management goal, and angling receives secondary emphasis (May et al. 2007). Regardless, special regulations that limit harvest can be very effective in protecting and enhancing target species (Gresswell 1986, Gresswell and Harding 1997). Furthermore, as concern for persistence of Yellowstone cutthroat trout has grown over the past several decades, the angler harvest has steadily declined, even where regulations provide for limited consumption.

## *Conservation Status of the Species in Region 2*

Results from the recent range-wide assessment for Yellowstone cutthroat trout (May et al. 2007) provide current information on distribution, genetic purity, and abundance of the subspecies in Region 2. In the region, Yellowstone cutthroat trout currently inhabit watersheds in the portions of the Shoshone and Bighorn national forests that lie in the Upper Yellowstone and Big Horn Geographical Management units (**Table 1**, **Table 2**, **Figure 1**, **Figure 2**, **Figure 3**, **Figure 4**, **Figure 5**). Historically, Yellowstone cutthroat trout were found in about 7,208 km of stream in the Upper Yellowstone Geographical Management Unit and 6,798 km in the Big Horn Geographical Management Unit. The subspecies currently occupies approximately 48 percent (3,495 km) of historical stream habitat in the Upper Yellowstone Geographical Management Unit and about 26 percent (1,772 km) in the Big Horn Geographical Management Unit (May et al. 2007).

Only a small proportion (4 percent) of the currently occupied streams in the Upper Yellowstone Geographical Management Unit is located in Region 2 (May et al. 2007). These stream segments (155 km occupied) lie in the Clarks Fork Yellowstone River watershed (4th level hydrologic unit) and flow through lands administered by the Shoshone National Forest. Introduced populations of Yellowstone cutthroat trout (largespotted form) have been established in four (previously barren of fish) small lakes (total surface area = 21 ha) located in the Clarks Fork Yellowstone River watershed (Shoshone National Forest). There are 28 other lakes inhabited by the subspecies in the Upper Yellowstone Geographical Management Unit, but except for four lakes in the Yellowstone Headwaters watershed (including Yellowstone Lake), these lakes support introduced populations (22 lakes) or populations with an unknown source (2 lakes) (May et al. 2007). There are no historical records of fish in any of these lakes with introduced populations.

In the Big Horn Geographical Management Unit, USFS Region 2 manages approximately 47 percent of the currently occupied streams (**Table 2**; May et al. 2007). Specifically, Region 2 forests administer lands in 10 watersheds (833 km occupied); only two occupied watersheds, the Lower Big Horn and the Upper Tongue, do not flow through National Forest System lands (May et al. 2007). Furthermore, only two of 107 lakes in the geographical management unit are reported to support native populations, but 104 of the historically barren lakes support introduced populations of Yellowstone cutthroat trout (May et al. 2007).

The largespotted form of the Yellowstone cutthroat trout occupies most (98 percent) of the stream habitat in the Upper Yellowstone Geographical Management Unit (May et al. 2007). The finespotted form of the Yellowstone cutthroat trout were limited to the Upper Yellowstone (28 km) and Clarks Fork Yellowstone River watersheds (25 km). According to May et al. (2007), the two populations in the Upper Yellowstone were native, but the population in the Clarks Fork Yellowstone River was derived from hatchery-reared, and genetically unaltered, progeny. The three largespotted Yellowstone cutthroat trout populations in the remaining 135 km of Clarks Fork Yellowstone River were also originally from introduced stocks (May et al. 2007). In total, however, about 88 percent of the remaining populations in the Upper Yellowstone Geographical Management Unit are aboriginal.

**Table 1.** Historical, current, conservation, and core populations of Yellowstone cutthroat trout located in subwatersheds of the Upper Yellowstone River and Big Horn River drainages that occur in the Shoshone and Bighorn national forests, USDA Forest Service, Rocky Mountain Region.

| Watershed Name | Watershed Code | Historical[1] | | Current[2] | | | Conservation[3] | | | Core[4] | | | Core | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | (HUC 4th field) | Miles | km | Miles | km | % Historical | Miles | km | % Historical | Miles | km | % Historical | Spotting[5] | Non-Native Species[6] |
| Clarks Fork Yellowstone | 10070006 | 525 | 845 | 96 | 155 | 18 | 84 | 135 | 16 | 76 | 122 | 14 | LS/FS | BRK,BRN,RBT,YSF |
| Upper Wind | 10080001 | 549 | 883 | 345 | 556 | 63 | 334 | 538 | 61 | 0 | 0 | 0 | LS/FS | BRK,BRN,RBT |
| Little Wind | 10080002 | 179 | 288 | 83 | 133 | 46 | 83 | 133 | 460 | 0 | 0 | 0 | NA | NA |
| Popo Agie | 10080003 | 130 | 209 | 29 | 46 | 22 | 29 | 46 | 22 | 0 | 0 | 0 | NA | NA |
| Upper Bighorn | 10080007 | 630 | 1,013 | 44 | 71 | 7 | 44 | 71 | 7 | 44 | 71 | 7 | LS/FS | BRK,RBT,YSL |
| Nowood | 10080008 | 555 | 894 | 11 | 18 | 2 | 5 | 9 | 1 | 3 | 6 | 1 | LS | None |
| Greybull | 10080009 | 312 | 501 | 231 | 372 | 74 | 231 | 372 | 74 | 231 | 372 | 74 | LS/FS | BRK,YSF |
| Bighorn Lake | 10080010 | 278 | 447 | 65 | 104 | 23 | 49 | 80 | 18 | 44 | 71 | 16 | LS | BRK,RBT |
| North Fork Shoshone | 10080012 | 271 | 436 | 253 | 408 | 94 | 14 | 23 | 5 | 0 | 1 | 0 | LS | None |
| South Fork Shoshone | 10080013 | 183 | 295 | 38 | 61 | 21 | 37 | 60 | 20 | 31 | 50 | 17 | LS/FS | BRK,BRN,YSF |
| Shoshone | 10080014 | 320 | 515 | 4 | 7 | 1 | 4 | 7 | 1 | 4 | 7 | 1 | LS | None |
| Lower Bighorn | 10080015 | 173 | 278 | 7 | 11 | 4 | 7 | 11 | 4 | 0 | 0 | 0 | NA | NA |
| Little Bighorn | 10080016 | 422 | 680 | 35 | 56 | 8 | 12 | 19 | 3 | 12 | 19 | 3 | LS/FS | BRK,RBT,YSL |
| Upper Tongue | 10090101 | 224 | 360 | 55 | 89 | 25 | 1 | 1 | 0 | 1 | 1 | 0 | LS | BRK |
| Total for Bighorn Geographic Management Unit | | 4,224 | 6,798 | 1,200 | 932 | 28 | 851 | 1,369 | 20 | 372 | 598 | 9 | | |
| Total for Upper Yellowstone and Bighorn Geographic Management Units | | 4,749 | 7,643 | 1,297 | 2,087 | 27 | 935 | 1,504 | 20 | 448 | 720 | 9 | | |

[1]Historical = Yellowstone cutthroat trout populations that occurred during initial European exploration of the Northern Rocky Mountains (approximately 1800).

[2]Current = populations managed primarily for recreational fishery values.

[3]Conservation = populations that may be slightly introgressed but have attributes worthy of conservation.

[4]Core = a genetically unaltered conservation population.

[5]LS = largespotted morphotype, FS = finespotted morphotype.

[6]BRK = brook trout; BRN = brown trout; RBT = rainbow trout; YSF = finespotted morph of Yellowstone cutthroat trout; YSL = largespotted morph of Yellowstone cutthroat trout.

**Table 2.** Ownership and land-management responsibility for watersheds supporting historical, current, conservation, and core conservation populations of Yellowstone cutthroat trout located in subwatersheds of the Upper Yellowstone River and Big Horn River drainages that occur in the Shoshone and Bighorn national forests, USDA Forest Service, Rocky Mountain Region.

| Ownership Group[1] | Watershed Name (4th Field HUC) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Clarks Fork Yellowstone -10070006 | Upper Wind -10080001 | Little Wind -10080002 | Popo Agie -10080003 | Upper Bighorn -10080007 | Nowood -10080008 | Greybull -10080009 | Bighorn Lake -10080010 | North Fork Shoshone -10080012 | South Fork Shoshone -10080013 | Shoshone -10080014 | Lower Bighorn -10080015 | Little Bighorn -10080016 | Upper Tongue -10090101 | Mean |
| **Historical Range (%)** | | | | | | | | | | | | | | | |
| BIA | 0 | 25 | 69 | 1 | 13 | 0 | 0 | 21 | 0 | 0 | 1 | 54 | 45 | 0 | 16 |
| BLM | 3 | 1 | 0 | 1 | 9 | 22 | 4 | 23 | 1 | 2 | 11 | 0 | 0 | 0 | 6 |
| NPS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 1 | 0 | 0 | 1 |
| PVT | 68 | 18 | 29 | 88 | 64 | 48 | 54 | 37 | 11 | 47 | 64 | 44 | 48 | 90 | 51 |
| STATE | 4 | 7 | 0 | 6 | 11 | 10 | 15 | 1 | 0 | 3 | 2 | 0 | 1 | 3 | 5 |
| USFS | 12 | 39 | 1 | 3 | 1 | 16 | 26 | 11 | 81 | 43 | 2 | 0 | 6 | 7 | 18 |
| USFWS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WATER | 12 | 10 | 1 | 0 | 1 | 4 | 1 | 4 | 3 | 4 | 19 | 1 | 0 | 0 | 4 |
| **Current Distribution (%)** | | | | | | | | | | | | | | | |
| BIA | 0 | 30 | 87 | 0 | 25 | 0 | 0 | 40 | 0 | 0 | 0 | 60 | 0 | 0 | 17 |
| BLM | 0 | 1 | 0 | 0 | 28 | 7 | 3 | 13 | 1 | 0 | 4 | 0 | 0 | 0 | 4 |
| NPS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| PVT | 9 | 13 | 5 | 0 | 31 | 23 | 48 | 19 | 9 | 23 | 31 | 40 | 23 | 3 | 20 |
| STATE | 1 | 8 | 0 | 0 | 3 | 69 | 15 | 2 | 0 | 0 | 1 | 0 | 7 | 4 | 8 |
| USFS | 87 | 37 | 8 | 100 | 10 | 0 | 35 | 26 | 87 | 77 | 64 | 0 | 70 | 92 | 50 |
| USFWS | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WATER | 3 | 11 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| **Conservation Populations (%)** | | | | | | | | | | | | | | | |
| BIA | 0 | 30 | 87 | 0 | 25 | 0 | 0 | 45 | 0 | 0 | 0 | 60 | 0 | 0 | 18 |
| BLM | 0 | 1 | 0 | 0 | 28 | 0 | 3 | 9 | 0 | 0 | 4 | 0 | 0 | 5 | 4 |
| NPS | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PVT | 9 | 13 | 0 | 0 | 31 | 5 | 48 | 12 | 0 | 230 | 31 | 40 | 32 | 95 | 24 |
| STATE | 1 | 8 | 0 | 0 | 3 | 0 | 15 | 0 | 0 | 0 | 1 | 0 | 19 | 0 | 3 |
| USFS | 87 | 38 | 8 | 100 | 10 | 95 | 35 | 34 | 100 | 77 | 64 | 0 | 49 | 0 | 50 |
| USFWS | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| WATER | 3 | 9 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

Table 2. Concluded.

| Ownership Group[1] | Clarks Fork Yellowstone -10070006 | Upper Wind -10080001 | Little Wind -10080002 | Popo Agie -10080003 | Upper Bighorn -10080007 | Nowood -10080008 | Greybull -10080009 | Bighorn Lake -10080010 | North Fork Shoshone -10080012 | South Fork Shoshone -10080013 | Shoshone -10080014 | Lower Bighorn -10080015 | Little Bighorn -10080016 | Upper Tongue -10090101 | Mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Core Conservation Populations (%) | | | | | | | | | | | | | | |
| BIA | 0 | 34 | NA | NA | 25 | 0 | 0 | 41 | 0 | 0 | 0 | NA | 0 | 0 | 9 |
| BLM | 0 | 0 | NA | NA | 28 | 0 | 3 | 10 | 0 | 0 | 4 | NA | 0 | 5 | 5 |
| NPS | 0 | 0 | NA | NA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | NA | 0 | 0 | 0 |
| PVT | 9 | 0 | NA | NA | 31 | 8 | 48 | 11 | 0 | 25 | 31 | NA | 32 | 95 | 26 |
| STATE | 1 | 0 | NA | NA | 3 | 0 | 15 | 0 | 0 | 0 | 1 | NA | 19 | 0 | 4 |
| USFS | 87 | 0 | NA | NA | 10 | 92 | 35 | 38 | 100 | 75 | 64 | NA | 49 | 0 | 50 |
| USFWS | 0 | 0 | NA | NA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | NA | 0 | 0 | 0 |
| WATER | 3 | 66 | NA | NA | 3 | 0 | 0 | 0 | 0 | 0 | 0 | NA | 0 | 0 | 7 |

[1]BIA = Bureau of Indian Affairs; BLM = Bureau of Land Management; NPS = National Park Service; PVT = Private; State = State of Wyoming; USFS = USDA Forest Service; USFWS = U.S. Fish and Wildlife Service; Water = Unidentified

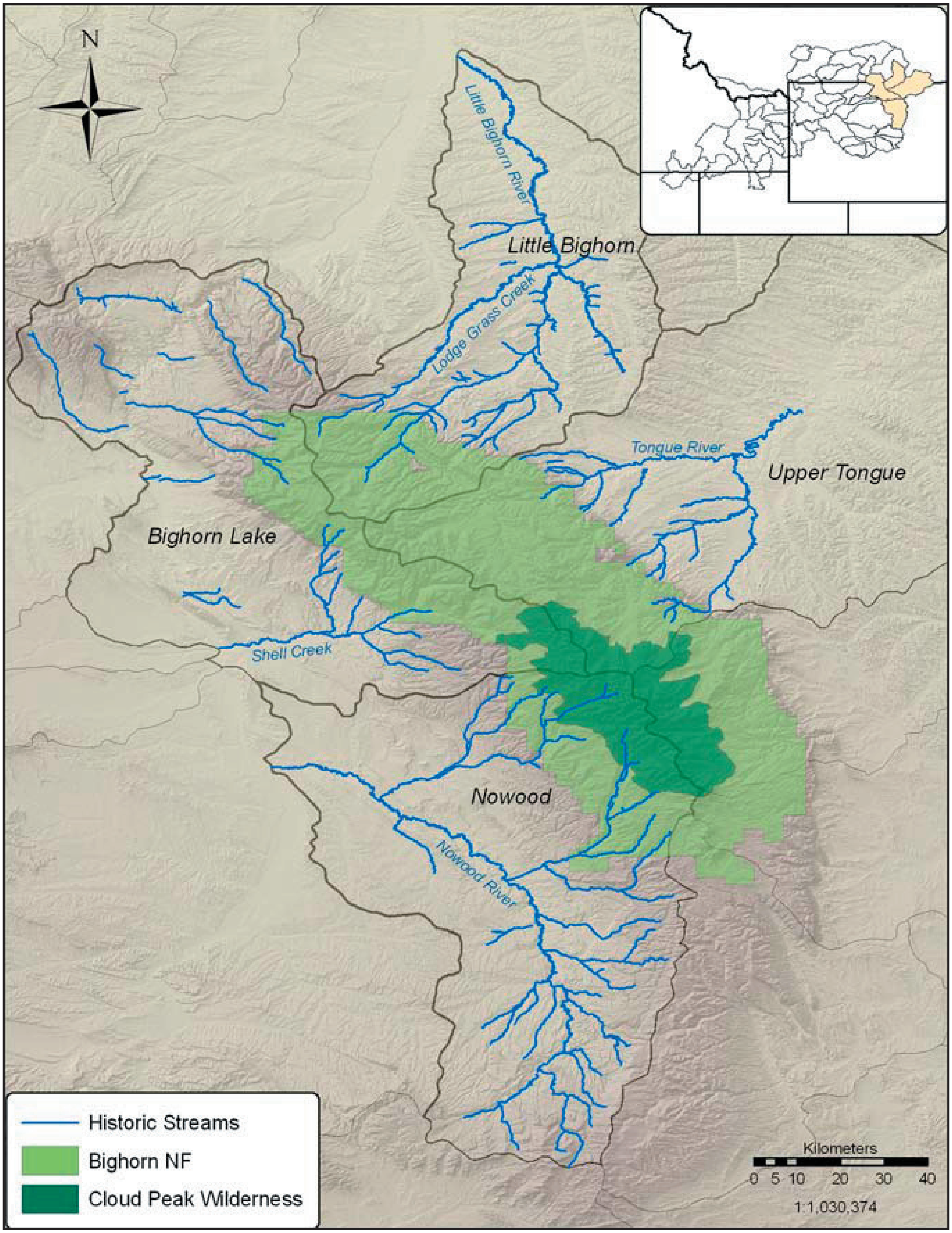


**Figure 1.** Historical Yellowstone cutthroat trout distribution in the Bighorn National Forest, USDA Forest Service, Rocky Mountain Region. Data obtained from May et al. (2007).

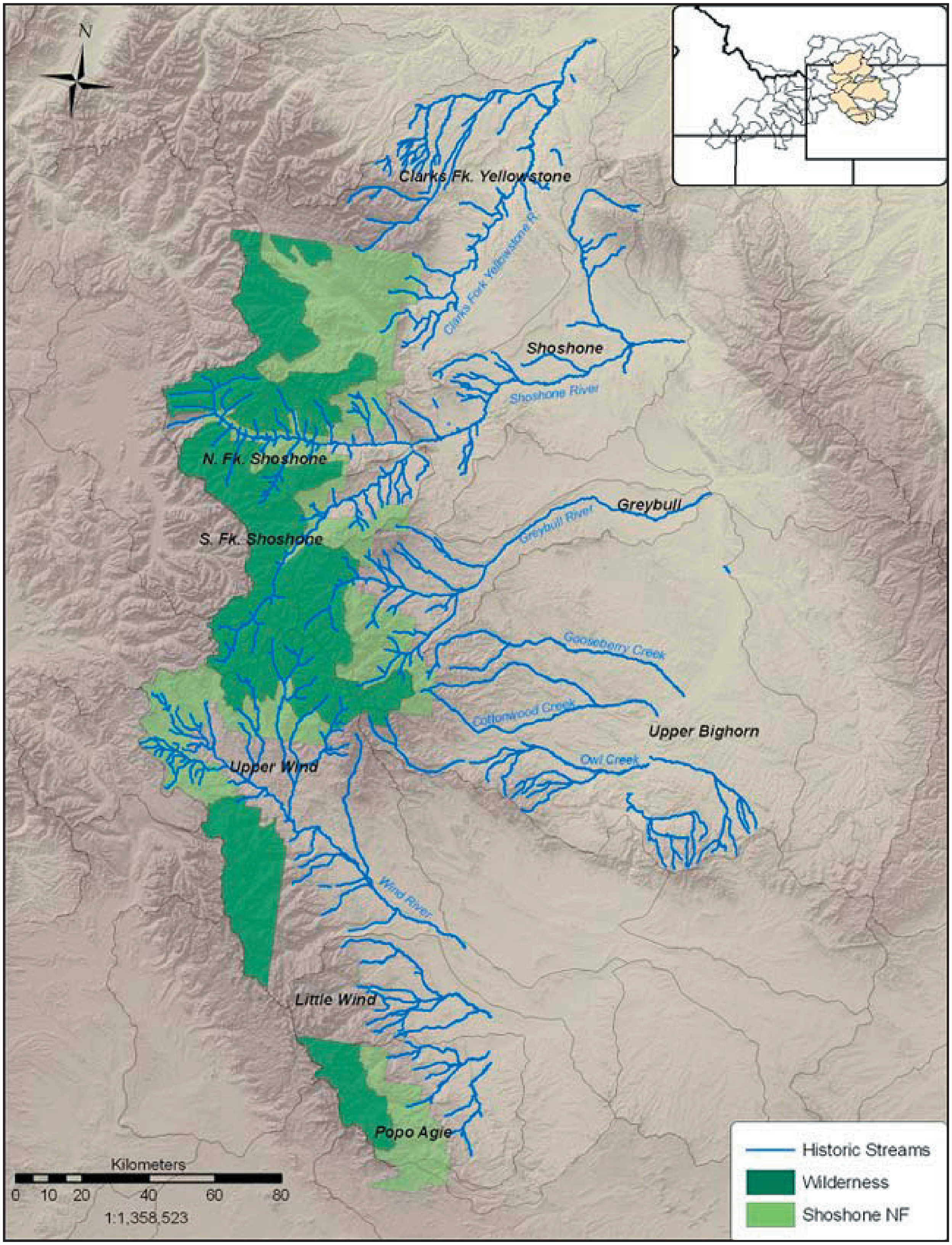


**Figure 2.** Historical Yellowstone cutthroat trout distribution in the Shoshone National Forest, USDA Forest Service, Rocky Mountain Region. Data obtained from May et al. (2007).

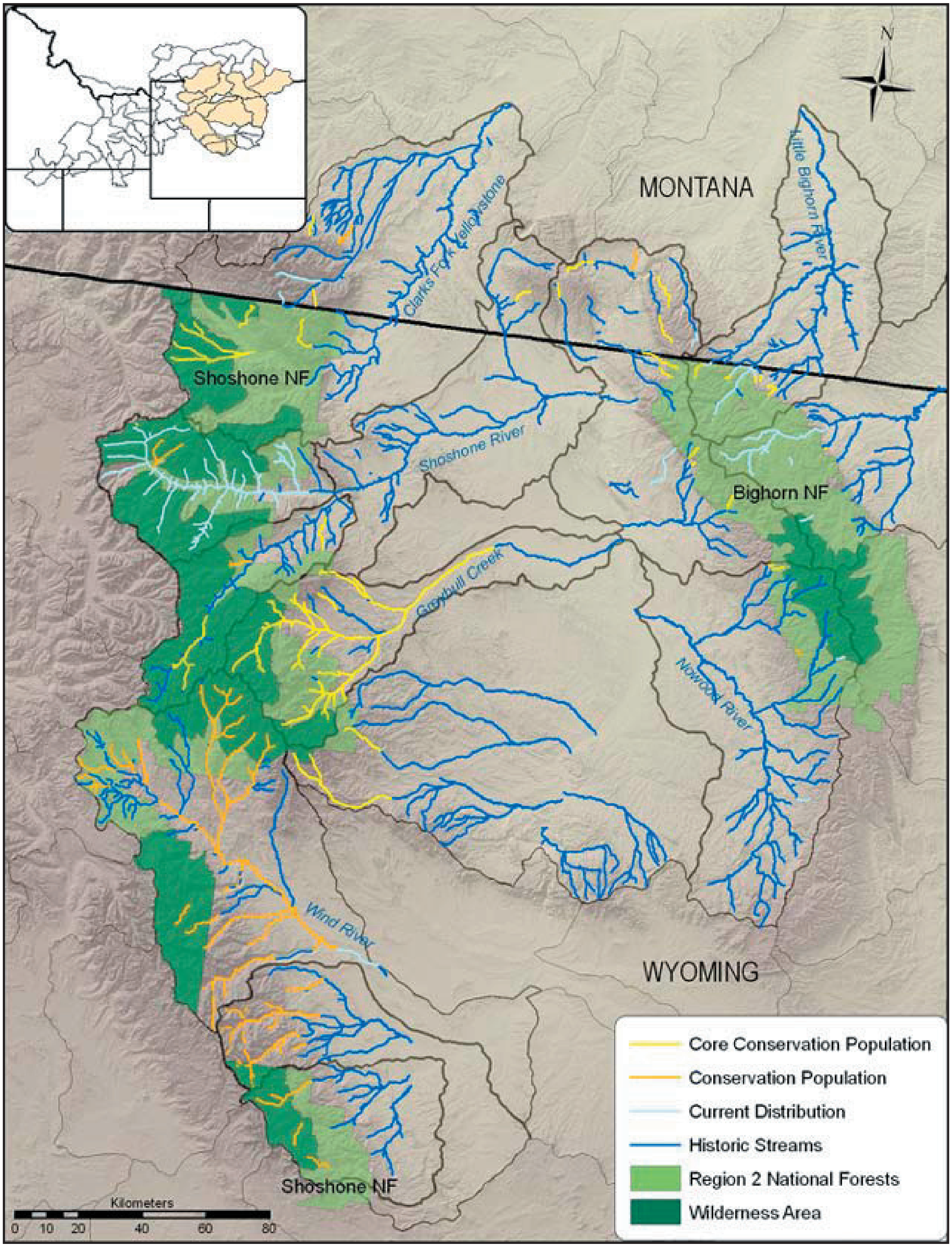


**Figure 3.** Yellowstone cutthroat trout distribution in the Shoshone and Bighorn national forests, USDA Forest Service, Rocky Mountain Region. Data obtained from May et al. (2007).

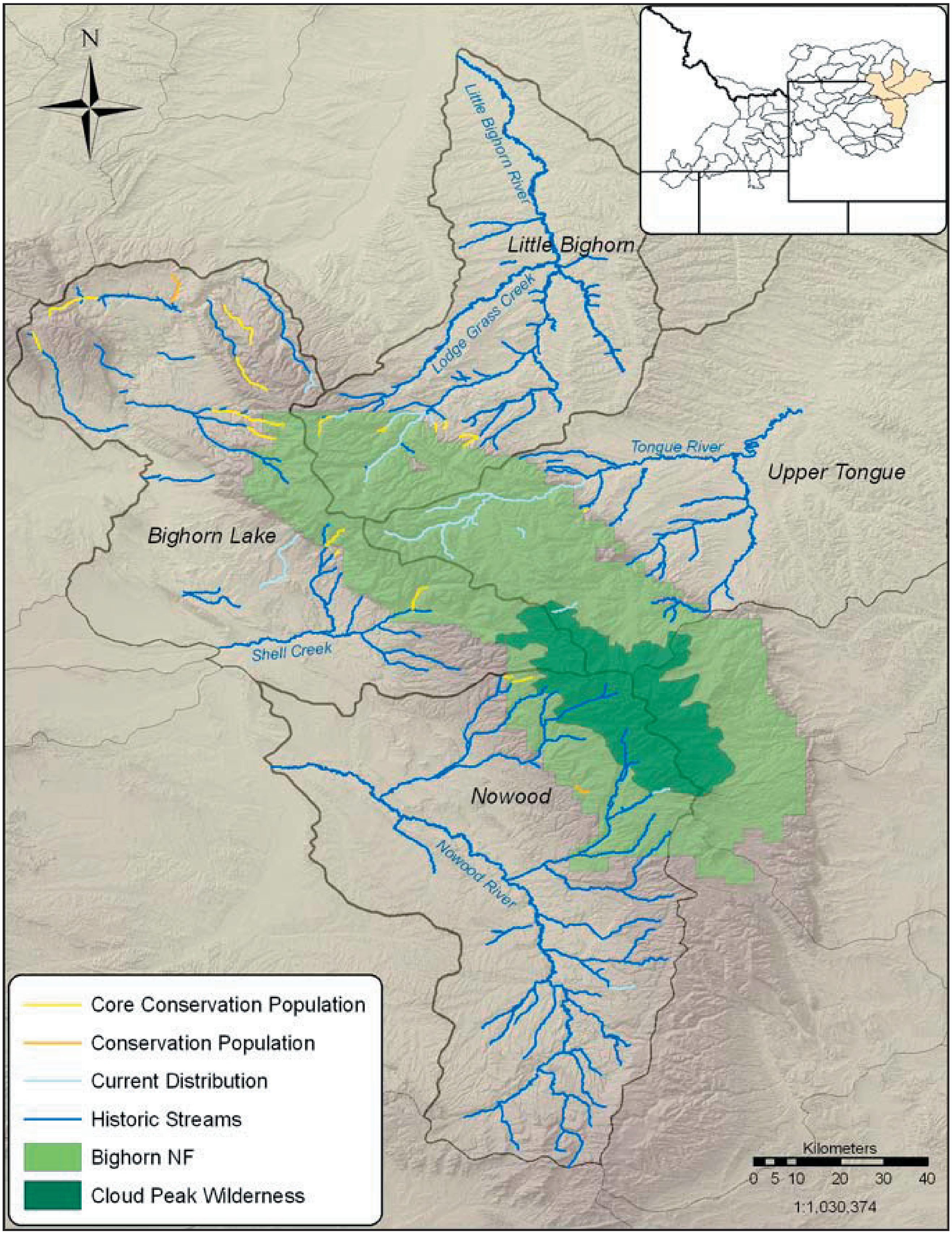


**Figure 4.** Yellowstone cutthroat trout distribution in the Bighorn National Forest, USDA Forest Service, Rocky Mountain Region. Data obtained from May et al. (2007).

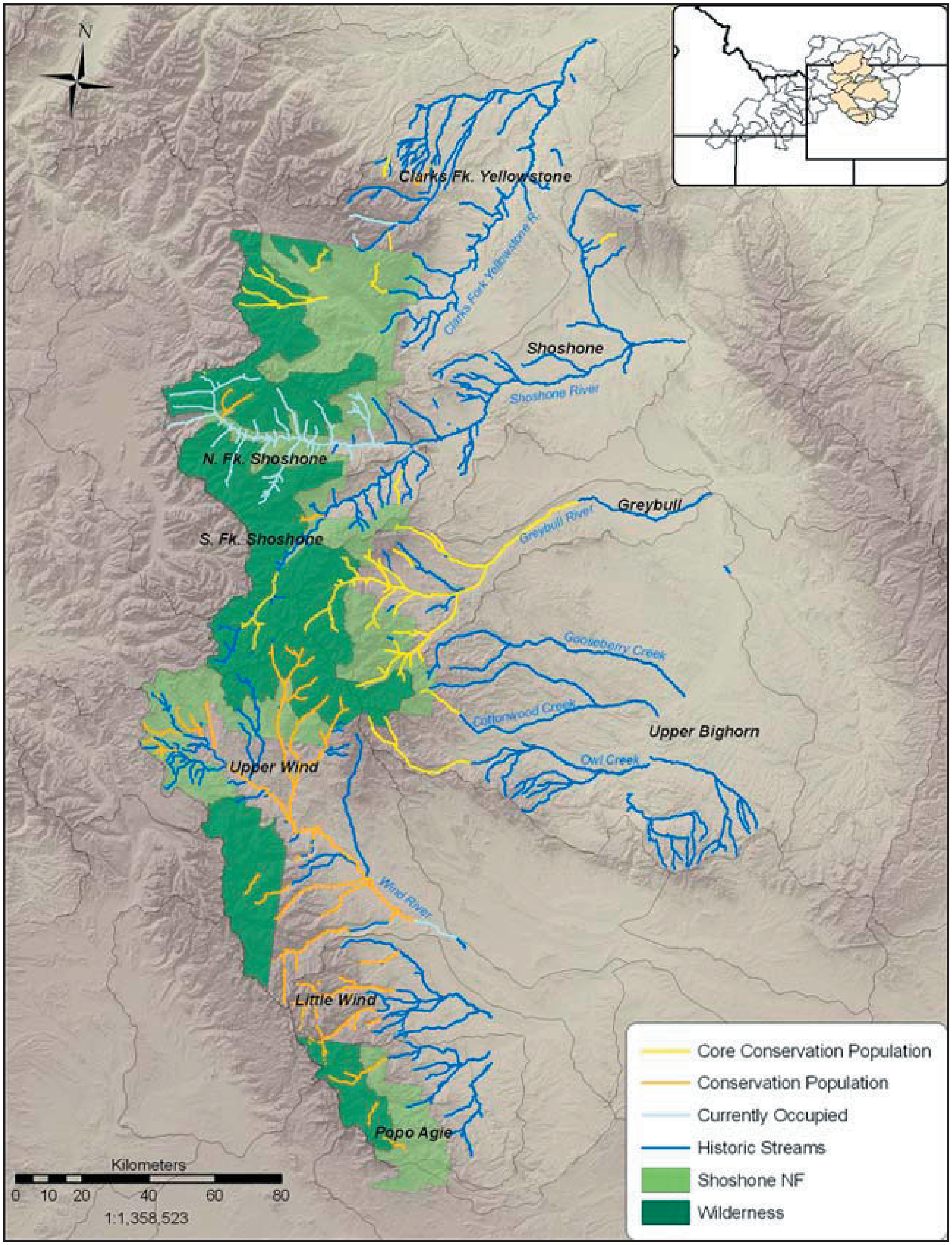


**Figure 5.** Yellowstone cutthroat trout distribution in the Shoshone National Forest, USDA Forest Service, Rocky Mountain Region. Data obtained from May et al. (2007).

According to May et al. (2007), Yellowstone cutthroat trout were native in approximately 1,095 km of the Big Horn Geographical Management Unit, and populations in about 632 km were established by the introduction of hatchery trout. Yellowstone cutthroat trout in the remaining 24 km of currently occupied habitat are of unknown origin. Curiously, the finespotted form of the Yellowstone cutthroat trout was reported in almost half (334 km) of putative native stream habitats in the geographical management unit (May et al. 2007), but this morphotype is indigenous to the Snake River watershed (Behnke 1992). On the other hand, both spotting patterns are found in the restored populations, and Kruse et al. (2000) reported that the non-indigenous finespotted form was stocked in these watersheds from 1972 to 1975. These data suggest that the portion of streams in the Big Horn Geographical Management Unit with native Yellowstone cutthroat trout may be much lower than reported.

Genetic testing in the Upper Yellowstone Geographical Management Unit indicated that 46 percent (6) of 13 stream populations tested were genetically unaltered; three introgressed populations exhibited >1 and ≤ 10 percent hybridization with rainbow trout (May et al. 2007). Of 13 untested populations, six were suspected to be unaltered, and seven were suspected to be hybridized. In total, there were 2,222 km of unaltered and suspected unaltered in the geographical management unit, and 1,053 km of hybridized, suspected hybridized, and sympatric (with rainbow trout). The Clarks Fork Yellowstone River watershed in the Shoshone National Forest had two unaltered populations (one tested and one suspected unaltered; 104 km total) and two suspected hybridized populations (51 km). Only one (6 ha) of 32 lakes in the Upper Yellowstone Geographical Management Unit was suspected hybridized; two of the remaining lakes (including Yellowstone Lake) were unaltered (34,610 ha), and three were suspected to be unaltered (322 ha). Four introduced lake populations (21 ha) in the Clarks Fork Yellowstone River watershed were suspected to be unaltered (May et al. 20007).

In the Big Horn Geographical Management Unit, 12 (75 percent) of the 16 populations that had been genetically tested were unaltered (May et al. 2007). One of the introgressed populations was >1 and ≤ 10 percent hybridized. Nine of the untested populations were suspected to be unaltered, and 10 were suspected hybridized; one population was sympatric (with rainbow trout). About 837 km of stream were occupied by unaltered/suspected unaltered Yellowstone cutthroat trout, and 925 km supported hybridized/suspected hybridized and sympatric populations. Only two lakes in the geographical management unit had been genetically tested; one population (4 ha) was unaltered and the other (21 ha) was hybridized. Seventy-one of the remaining lakes (835 ha) supported suspected unaltered populations, and 34 lakes (4,657 ha) were occupied by suspected hybrid populations (May et al. 2007). Most of these lakes are in the Upper Wind and Little Wind watersheds and were historically fishless.

About 1,070 km of stream in the Clarks Fork Yellowstone River watershed have been stocked with Yellowstone cutthroat trout (largespotted form only), but there are no records on non-indigenous fish stocking in this portion of the Upper Yellowstone Geographical Management Unit (Table 1; May et al. 2007). Both largespotted and finespotted forms have been stocked in the Pryor River watershed (76 km). There are no records of stocking in approximately 1,070 km of the geographical management unit, mostly in the Yellowstone Headwaters and Upper Yellowstone watersheds, but non-indigenous fish have been stocked in almost 1,260 km of stream (Shields and Stillwater watersheds). Only three lakes in this geographical management unit (Stillwater watershed) have been stocked with non-indigenous fish. There are no stocking records for 13 lakes, and according to May et al. (2007), 16 lakes (including Yellowstone Lake) were stocked only with the largespotted form of Yellowstone cutthroat trout. Official records from Yellowstone National Park do not support this statement, however, and Gresswell and Varley (1988) report that mountain whitefish, landlocked Atlantic salmon (*Salmo salar*), and rainbow trout were all officially stocked in the lake between 1889 and 1909. Furthermore, redside shiner, lake chub, and longnose suckers all became established in the lake prior to the 1960's (Gresswell and Varley 1988), and lake trout were discovered in the lake in 1994 (Kaeding et al. 1996). These non-salmonid fishes were all introduced unofficially.

There are no stocking records for 17 populations (representing 510 km of stream) in the Big Horn Geographical Management Unit (May et al. 2007). Of the remaining 23 populations with records, 16 received plants of non-indigenous species (1,068 km), and seven were stocked only with Yellowstone cutthroat trout (184 km) (May et al. 2007). The presence of the finespotted form in virtually all of the watersheds in this geographical management unit suggests that stocking occurred in many places where it has not been documented. Non-indigenous fish were stocked in nine lakes in the Big Horn Geographical Management Unit (4,752 ha), and there are no stocking records for five lakes (353 ha) (May et al. 2007). Stocking records indicate that six lakes in the Upper Wind and Little Wind watersheds received only Yellowstone cutthroat trout, but both forms are found (two lakes with only the largespotted form, two with only the finespotted form, and two with both).

There are six conservation populations of Yellowstone cutthroat trout in the Clarks Fork watershed, and five were ranked as core conservation populations (genetically unaltered) (May et al. 2007). Three of these core conservation populations were located in non-networked systems (39 km total), one was in a weakly networked system (7 km), and one was in a strongly networked system (76 km). The other conservation population (non-core) was a non-networked system (13 km). All of the core conservation populations had limited risk for disease (May et al. 2007). Although risk of hybridization was also limited, four of the populations (including the non-core population) were sympatric with non-indigenous fishes. Interestingly, the one strongly networked population had rainbow trout and the non-indigenous finespotted form of Yellowstone cutthroat trout in the system, but only 22 percent of the system was affected. The two populations (24 km total) without non-indigenous fishes were isolated by a barrier to upstream fish movement. Fish density in four of the core conservation populations and the non-core conservation population was about 60 fish per km; the strongly networked core conservation population exceeded 400 fish per km. Overall population health scores (May et al. 2007) ranged from low (two populations) to moderate (four populations). Low scores for potential population productivity dropped the ranking of the strongly networked core population to moderate overall population health (May et al. 2007).

There are 113 conservation populations of Yellowstone cutthroat trout in the Big Horn Geographical Management Unit (**Table 1**), and 30 were ranked as core conservation populations (genetically unaltered) (May et al. 2007). Core conservation populations occurred in 73 percent (8) of the 11 watersheds in the unit, including the Upper Big Horn, Nowood, Greybull, Big Horn Lake, North Fork Shoshone, South Fork Shoshone, Shoshone, and Little Big Horn watersheds. Twenty-four (80 percent) of the core populations were located in systems that were not networked (210 km); one was weakly networked (6 km), three were moderately networked (174 km), and two populations were strongly networked (206 km). One strongly networked population in the North Fork Shoshone watershed had a known or probable unique life history. Of the non-core conservation populations (83), 65 occurred in non-networked systems (142 km), 10 were weakly networked (161 km), five were moderately networked (77 km), and two were strongly networked (352 km).

All but two of the core conservation populations had limited risk of disease; these two populations were rated minimal disease risk (May et al. 2007). There was no risk of hybridization for 17 of the populations, but two supported hybridizing species >10 km away, eight supported hybridizing species within 10 km, and three were sympatric with hybridizing species. Fourteen of the core populations were sympatric with non-indigenous fishes; brook trout were most common (nine populations), followed by the finespotted form of the Yellowstone cutthroat trout (eight populations), rainbow trout (four populations), and brown trout (two populations). Two or more non-indigenous fishes occurred in eight of the watersheds. A barrier to upstream fish movement isolated eighteen of the populations, but Yellowstone cutthroat trout were sympatric with non-indigenous fishes in seven of these populations. Fish densities were low for these core populations, <175 per km in all but two of the populations. Densities of the two moderately networked core conservation populations were between 340 and 470 fish per km.

In general, data suggest that even where core conservation populations remain in the Big Horn Geographical Management Unit, in the absence of management interaction, probability of persistence may be limited (sensu Hilderbrand and Kershner 2000b; Kruse et al. 2001; Peterson et al. 2008). Overall population health scores (May et al. 2007) ranged from low (20 populations) to moderate (10 populations). Low network connectivity scores (24 populations) and low temporal stability scores (20 populations) were the primary factors that lowered the ranking of the core populations (May et al. 2007).

## *Potential Management of the Subspecies in Region 2 of the USDA Forest Service*

### Implications and potential conservation elements

The Yellowstone cutthroat trout was historically found in many portions of the Yellowstone River drainage in the Shoshone and Bighorn national forests in USFS Region 2 (**Table 1**, **Figure 1**, **Figure 2**, **Figure 3**, **Figure 4**, **Figure 5**; May et al. 2007). Throughout the 20th century, introduction of non-indigenous fishes (resulting in hybridization, predation, disease, and interspecific competition), habitat degradation (e.g., water diversions, grazing, mineral extraction, and timber harvest), and angler harvest resulted in declines in distribution and abundance of Yellowstone cutthroat trout, and extirpations were common. Population declines have been greatest in larger, low-elevation streams. Remote location has probably contributed to the preservation of remaining populations, and in much of this area, public ownership (in the form of national parks and wilderness areas) has provided habitat protection that is lacking in more accessible, low-elevation portions of the range. For example, state and federal agencies administer over 70 percent of the lands that support Yellowstone cutthroat trout (i.e., current distribution, conservation populations, and core populations), and the Shoshone and Bighorn national forests manage 50 percent of these lands (Table 2). Historically, 51 percent of the lands supporting Yellowstone cutthroat trout occurred on private lands, but currently, only about 20 percent of the subspecies' current distribution is found on private lands.

Management actions (e.g., special regulations, riparian fencing, culvert replacement, bank stabilization, instream habitat restoration, population restoration/expansion, and chemical removal of competing/hybridizing species) initiated in the past several decades appeared to stabilize, and in some cases improve the distribution of the Yellowstone cutthroat trout. Despite the presence of numerous populations, however, most genetically unaltered assemblages (core conservation populations) are found in fragmented habitats in headwater streams where abundance is low (May et al. 2007). Recent introductions of non-indigenous species (e.g., lake trout; New Zealand mud snail; and *Myxobolus cerebralis*, the causative agent of whirling disease) and persistent drought in the Northern Rocky Mountains have increased concern about many populations that had previously been deemed secure. There is little doubt that changes in climate and the concomitant shifts in timing and availability of water will continue to exacerbate the probability that the range of the subspecies will decline in the region. As water temperatures increase, current Yellowstone cutthroat trout habitat may become more conducive for non-indigenous fishes (e.g., brown trout and rainbow trout), and current abiotic cues that serve to reinforce reproductive isolation between hybridizing species (e.g., rainbow trout and cutthroat trout) may be disrupted. As habitat in headwater streams becomes seasonally marginal, Yellowstone cutthroat trout may be forced lower where non-indigenous trout are more prevalent. Furthermore, the potential for upstream movement may be limited because of habitat alterations (e.g., culverts and diversions) or presence of non-indigenous brook trout.

Current estimates of status and distribution of the Yellowstone cutthroat trout suggest that it may be impossible to restore the subspecies to 100 percent of its historical range. Furthermore, it appears that the proportion of the range that supports healthy, secure core conservation populations is low, and given the range of potential factors that negatively affect Yellowstone cutthroat trout populations, persistence of core populations is not certain. Persistence of the subspecies may benefit from a hierarchical approach that includes (1) protection of the strongest core conservation populations; (2) enhancement by reconnecting and replicating the core populations wherever possible; and (3) restoration of populations when practical.

According to the most recent status assessment, 14 core conservation populations of Yellowstone cutthroat trout in streams that are administered by Region 2 have a moderate health classification, and none were rated in the high category (May et al. 2007). Protection of these remaining strongholds of genetically unaltered individuals is probably the number one management priority for this area. As noted above, once a population has been altered, restoration is uncertain. Preventing invasion of non-indigenous fishes, from either natural (migration from previously established populations) or anthropogenic (transplanting) pathways, is critical. To avoid introgression with non-indigenous taxa (including Yellowstone cutthroat trout from other portions of the historical range), stocking non-native fishes to support recreational angling in streams and lakes should be precluded. In cases where non-indigenous fishes occur in the watershed, physical isolation of the remaining cutthroat trout by barrier construction may be required. Alternatively, in some cases it may be possible to remove the non-indigenous fishes by either physical or chemical means. It is also important to consider prohibiting new management activities that would directly (e.g., pollution) or indirectly (e.g., habitat destruction) compromise these populations of Yellowstone cutthroat trout.

There are 22 core conservation populations with a low health classification in Region 2 (May et al. 2007). Although it is important to prevent further degradation in these areas, efforts focused on population enhancement are critical. Perhaps the most important management action in many of these systems is the removal of non-indigenous fishes where they co-occur with Yellowstone cutthroat trout. Current evidence suggests that taxa that can hybridize with the Yellowstone cutthroat trout (e.g., rainbow trout and other cutthroat trout subspecies) pose the greatest threat to persistence of the native Yellowstone subspecies, and to reduce this threat, removal of non-indigenous fishes in these systems should be a priority. Where hybrids occur, they should also be targeted for removal in order to improve genetic integrity. As noted above, either physical or chemical means may be used, and habitat conditions generally dictate which is appropriate.

Specific habitat management activities focused on improving riparian and stream channel conditions can be useful for improving habitat conditions (Winters et al. 2004b) for core conservation populations of Yellowstone cutthroat trout. Where possible, reconnecting stream segments within the network can improve the probability of persistence by reducing the threats posed by catastrophic disturbance events (e.g., fire and floods), and concomitantly, increasing the size and complexity of habitat will foster the expression of more complex and less common life-history types. In many cases, the removal of non-indigenous species will be necessary before reconnecting disparate portions of a stream network by removing anthropogenic barriers to fish movement (e.g., culverts and water diversion structures). This is especially important where barrier removal would allow non-indigenous fishes to access habitat currently occupied by allopatric assemblages of Yellowstone cutthroat trout. Until removal of non-indigenous species occurs, connectivity may require human translocations to maintain an effective population size ($N_e$; Fausch et al. 2006; Peterson et al. 2008).

Replication of core conservation populations (i.e., introduction into a watershed where Yellowstone cutthroat trout did not occur historically) is another strategy that can greatly improve the probability of persistence of Yellowstone cutthroat trout, especially in the face of potential demographic collapse associated with climate change. Of the core conservation populations in Region 2 of the USFS, 27 (77 percent) occur in non-networked systems that may be vulnerable to catastrophic disturbance events. Replication entails introductions into headwater drainage where Yellowstone cutthroat trout did not occur historically because of passage barriers. Although there may be ethical issues associated with this type of management activity, the potential benefits to Yellowstone cutthroat trout persistence may substantially outweigh negative effects on native invertebrate communities. For example, fishless headwater streams often comprise over 60 to 80 percent of the cumulative channel length in mountainous areas (Schumm 1956, Shreve 1969), and redundancy of invertebrate communities is often high. Conversely, many of the fishless streams in the western United States occur in wilderness areas where current management policies prohibit the introduction of any fish into previously fishless waters (except where stocking preceded wilderness designation; Anonymous 2006).

Restoration of Yellowstone cutthroat trout populations in the historical range may be the most difficult option available to managers. Extensive planning and monitoring at the watershed scale are integral to this type of restoration activity. Total extirpation of introduced non-indigenous fishes is often required, but the expense of renovation with piscicides is frequently prohibitive, even in areas where it may be technically possible. Furthermore, the probability of successfully removing non-indigenous fishes is often low, and most projects in streams require two or more applications (Meronek et al. 1996, Finlayson et al. 2002). In addition, social issues sometimes lead to legal challenges to renovation projects (Finlayson et al. 2005). Habitat degradation can be severe where Yellowstone cutthroat trout have been extirpated, and restoration may require decades to centuries (Frissell 1997). Because of the extensive amount of time necessary to observe anticipated results, maintaining support for such projects is often problematical.

One important management activity that crosses the boundary between protection and restoration is related to system connectivity. Although fragmentation may greatly reduce the probability of persistence of isolated Yellowstone cutthroat trout populations, the presence of barriers to upstream fish movement is often the only reason that non-indigenous fishes have not invaded upstream portions of the watershed. Removal of barriers may increase the probability of persistence and allow for life-history expression (e.g., migratory life-history types) that is suppressed by features that prevent passage (natural and anthropogenic); however, in many cases, providing access to non-indigenous fishes may be a more significant short-term threat. Purposely isolating populations by the construction of barriers may increase short-term probability of persistence, but in some cases, this alternative has negative long-term consequences. In an effort to provide a decision-support tool for making management decisions associated with this issue, Peterson et al. (2008) recently developed a Bayesian belief network that evaluates environmental factors influencing the species pool, interactions among the species, and the effects of isolation on the targeted cutthroat trout population.

Of course, all of the management actions focused on the persistence of Yellowstone cutthroat trout are predicated on access to information on the distribution and abundance of genetically unaltered populations of the subspecies. This information requires continued searches for unsampled populations until all of the potential current range of Yellowstone cutthroat trout has been evaluated. This can be done in a systematic fashion; however, it is critical to develop a range-wide plan with a projected completion date. Identification and testing will need to be coordinated across a variety of state and federal agencies, on public and private lands.

An integrated monitoring plan is the second vital component of management that must be developed with cooperation of state and federal management and scientific support agencies. Although there has been a significant improvement in the variety and quality of the data being used to assess the status of the Yellowstone cutthroat trout, a more statistically robust sampling protocol is necessary for expanding the scope of inference associated with future assessments to the entire range of the Yellowstone subspecies. Because trend detection is the ultimate goal of most assessments, it is critical to develop a design that includes a network of probabilistically chosen sites that can be monitored consistently through time. Additionally, an independent effectiveness-monitoring program is necessary for evaluating habitat improvement, non-indigenous species removal, and Yellowstone cutthroat trout introduction/reintroduction projects.

## Tools and practices

### *Range-wide species distribution*

In the last decade, protocols for species inventories have become more scientifically rigorous and spatially extensive, especially for the interior cutthroat trout (e.g., May and Albeke 2005, Shepard et al. 2005, May et al. 2007). Development of standardized protocols has promoted acquisition of new information concerning distribution and abundance of Yellowstone cutthroat trout, and coupled with increased genetic sampling, it has been possible to better delineate the extent of genetically unaltered populations. Current procedures incorporated the National Hydrography Dataset as the base for the assessment at the 1:24,000 scale, and all population data were georeferenced (May et al. 2007).

Despite the improvements, however, current protocols are not based on a statistically rigorous sampling framework that provides objective assessment of presence/absence, genetic integrity, or population abundance. Perhaps the most urgently needed, and yet most easily obtainable, information relates to the current distribution and genetic status. A variety of protocols have been used successfully (Harig and Fausch 2002, Bateman et al. 2005, Young et al. 2005) to assess the distribution of fishes in a watershed. Although the most appropriate method for any particular study is related to objectives and available resources, it is important to maintain comparability among studies. Critical elements for establishing the extent of fish in a watershed include a systematic sample of all available habitats and the use of fish collection/observation techniques that provide a known probability of individual capture (Bayley and Petersen 2001).

Combining surveys of distribution with the collection of tissue for genetic analysis provides a means to improve understanding of genetic integrity of remaining populations. Genetic techniques for identifying unaltered Yellowstone cutthroat trout are well established, and collecting and storing tissue in the field is simple and straightforward (Cegelski et al. 2006). Tissue samples should also be collected from individual watersheds in a probabilistic manner so that results can be used for statistical comparisons among sites and through time. In situations where the cost of analysis is prohibitive, samples can be archived for future examination.

In many cases, selection of sample sites for species distribution and genetic integrity has not used a probabilistic sampling procedure, and therefore, inference is limited. Although it could be argued that the number of samples collected to assess Yellowstone cutthroat trout distribution is great enough that it represents the actual distribution on the landscape, without an objective statistical design, it will be difficult to assess changes through time. Furthermore, systematic errors are more frequent when sampling is primarily happenstance, and it is possible that the assemblages with unique characteristics will be overlooked.

### *Habitat inventory*

Numerous habitat assessment protocols have been developed for the assessment of habitat quality in streams (e.g., Frissell et al. 1986, Hankin and Reeves 1988, Kruse et al. 1997), and more recently robust statistical designs have been developed to expand estimates to the landscape scale (Larsen et al. 2004, Winters et al. 2004a, Gresswell et al. 2006). Although most studies of fish habitat are conducted at the local scale (e.g., transects and channel units;

see Armantrout 1998), this may be inappropriate for organisms, such as salmonids, that require a variety of habitats depending on season or life stage (Northcote 1997). Unfortunately, protocols for examining these data in a broader context have not been adequately developed (Imhof et al. 1996, Poole et al. 1997), but recent efforts using a nested approach that incorporates information from multiple spatial scales may prove useful. The lack of information at the landscape scale is often the result of a combination of factors, including (1) the expense and logistical difficulties associated with research at broad spatial scales; (2) extensive heterogeneity that occurs at broader spatial scales; (3) difficulties associated with experimentally manipulating landscapes; and (4) previous failure to recognize the potential importance of landscape patterns on organisms (Gresswell et al. 2004).

Although the decision to assess fish habitat in conjunction with initial evaluation of species distribution should be based on specific study objectives, these data can be used to help explain observed distributions. Furthermore, such data are useful for identifying factors that may limit the occurrence of the Yellowstone cutthroat trout and provide the basis for future monitoring. These potential applications underscore the importance of a sound statistical sampling framework for initial studies and provide greater justification for the added costs for these activities.

One recent analysis used a hierarchical approach for assessing habitat quality and management opportunities in the current range of the Yellowstone cutthroat trout (Winters et al. 2004a). A classification scheme was developed to arrange small watersheds into groups based on productivity and abundance of aquatic, riparian, and wetland resources and their response to disturbance. Analysis of historic and current anthropogenic activities provided regionally consistent comparisons of effects among watersheds at a variety of spatial scales. This type of analysis is critical for identifying restoration and monitoring priorities for the Yellowstone cutthroat trout in the context of broader ecosystem management constraints.

### *Population and habitat monitoring*

Recent efforts to evaluate Yellowstone cutthroat trout abundance have evolved from a qualitative assessment of density to population estimates of mature individuals in each habitat segment. Standard mark-recapture and depletion techniques are more frequently used to provide estimates of abundance and precision (Budy et al. 2007), and current assessment protocols require information necessary to identify the technique used for each sample. Estimates for lake populations have not been included in range-wide status assessments (May et al. 2007). Gresswell et al. (1997b) successfully used a single-census Petersen estimator to obtain precise estimates of salmonids in remote small lakes, and this technique may be useful for developing quantitative estimates of abundance for some lake populations of Yellowstone cutthroat trout. On the other hand, the effort required to obtain precise population estimates may not be warranted for many lake populations. Relative abundance or angler-use information may provide adequate information to develop preliminary assessments.

At this point, statistically robust protocols for evaluating changes through time have not been incorporated in the Yellowstone cutthroat trout status assessments (May et al. 2007). Current evaluations have relied on resampling index sites that have been previously assessed for a variety of reasons (e.g., Meyer et al. 2003b), and although the studies are useful, efforts to expand statistical inference are lacking. Recent protocols developed for monitoring habitat quality in salmon streams in the Pacific Northwest (Larsen et al. 2004) provide a template that can be used to develop a statistical sampling design for comparing population trends through time. When funds are limited, restoration activities may receive higher priority than landscape-scale monitoring; however, monitoring effects of individual restoration projects is critical for evaluating outcomes and maintaining public support for such activities.

Although measurement error at a particular location (i.e., error associated with population estimates and determination of presence/absence) can influence estimates of abundance and/or occurrence at an individual site, obtaining an unbiased status assessment requires consideration of error associated with the selection of sample sites (Olsen et al. 1999, Stevens and Olsen 2004). Information from a site, or a group of sites, has little inferential value (regardless of scale) if sites were not selected using a probability-based sampling protocol. Over the past two decades, substantial progress has been made in the development of robust statistical sampling designs for unbiased ecological assessments of aquatic systems. For example, the Environmental Monitoring and Assessment Program, developed by the U.S. Environmental Protection Agency, formalized a protocol for probability-based sampling design that is useful for monitoring and assessment of status and trends of aquatic species in lakes and rivers at multiple spatial scales (Urquhart et al. 1998). Recent evaluation of spatial and temporal variation in trend analysis suggests that consistent annual monitoring of 30 to 50 sites can detect subtle changes in habitat condition that can influence species distribution (Larsen et al. 2004). Furthermore, probability-based sample selection has also been successfully applied at the watershed scale (Gresswell et al. 2004, Gresswell et al. 2006).

### *Population and habitat management*

**Isolation-stream network connectivity:** The ubiquity of non-indigenous species throughout the range of the Yellowstone cutthroat trout represents a pernicious threat to the persistence of the subspecies, and therefore, isolation of genetically unaltered populations may be necessary. Unfortunately, isolation and fragmentation, especially in small headwater drainages, substantially increase the risk of demographic collapse (Kruse et al. 2001) following catastrophic disturbances (e.g., wildfire and subsequent flooding and debris flow events) or as a result of gradual reductions in habitat suitability related to climate change (i.e., ramp disturbances such as increased water temperature and prolonged drought). Furthermore, curtailing upstream fish passage directly affects individuals that move, eventually causing the extirpation of mobile life-history types.

Unfortunately, it is difficult to predict the minimum catchment size necessary to support fish populations indefinitely. For example, evidence suggests that demographic isolation of coastal cutthroat trout upstream from dispersal barriers in a headwater stream (2,200 ha) has resulted in decreased genetic diversity (Wofford et al. 2005). Regional genetic diversity among coastal cutthroat trout populations in 27 headwater catchments (500 to 1,000 ha) is affected by differences in within-watershed complexity and connectivity (Guy et al. 2008). On the other hand, these systems have supported coastal cutthroat trout for thousands of years (Guy et al. 2008). In contrast, populations of Gila trout and Bonneville cutthroat trout in small headwater streams have been extirpated following wildfire and accompanying postfire floods (Rinne 1996, J. Kershner, personal communication, 2006). Furthermore, Dunham et al. (1997) found Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*) in 89 percent of 47 networked systems, but the subspecies was present in only 32 percent of 72 fragmented (isolated) catchments.

Decisions concerning reconnecting stream networks that have been inadvertently fragmented by previous anthropogenic activities (e.g., impassable road culverts or dams) or purposely blocked to prevent invasions by non-indigenous fishes must be evaluated on a case by case basis (Peterson et al. 2008). Fausch et al. (2006) recently suggested four key considerations that provide a framework for examining the tradeoffs between isolation and invasion (related to stream network connectivity). These factors include (1) the conservation value of a particular native salmonid population; (2) vulnerability of the population to invasion and displacement; (3) probability of persistence following isolation; and (4) prioritization among multiple populations with conservation value. In any event, rigorous monitoring following either decision (i.e., intentional isolation or stream network reconnection) should be required so that the effects of the management action (both positive and negative) can be evaluated. The concept of adaptive management (Walters 1986) is especially appropriate as a guiding principle for this type of management decision so that future outcomes eventually become more predictable.

**Removal:** Although the removal of non-indigenous species is difficult and often expensive (Rinne and Turner 1991, Meronek et al. 1995), this management activity may be the only viable option for expanding the distribution of Yellowstone cutthroat trout in the historical range of the subspecies (Finlayson et al. 2005). In cases where installation of fish passage barriers is not warranted because of demographic risks to the isolated Yellowstone cutthroat trout, removal of non-indigenous fishes from the stream network may be an appropriate alternative (Fausch et al. 2006). Where distributions of native and non-indigenous fishes overlap, removal of native fish by electrofishing prior to piscicide application has been successful (Renner 2005).

Antimycin and rotenone are the most commonly used piscicides. Current production issues have reduced the availability of antimycin, and rotenone has been used more frequently in recent years because of greater availability and lower price (Finlayson et al. 2002). Electrofishing may be effective for removing non-indigenous fishes in some cases where the target area is small and habitat is simple (Kulp and Moore 2000; Shepard et al. 2002). This technique often does not result in complete extirpation of target species (Thompson and Rahel 1996, Meyer et al. 2006a), but frequently repeated removals may be effective for increasing short-term survival of native Yellowstone cutthroat trout when hybridization is not a concern.

Success of removal projects is often limited by the size and complexity of the target watershed. Furthermore, where watershed ownership is mixed between private and public entities, it is often difficult to obtain consensus among stakeholders for conducting projects involving the application of piscicides. Initial success of removal and reintroduction projects in headwater streams on publicly owned lands may be necessary to demonstrate the feasibility these activities for restoring Yellowstone cutthroat trout where non-indigenous fishes have become established.

**Redundancy:** Because most of the remaining genetically unaltered populations of Yellowstone cutthroat trout currently inhabit small isolated headwater streams, it is important to increase the number of these populations. In some cases, this can be accomplished by introducing native fishes into streams that did not historically support fishes. This strategy is sometimes coupled with the removal of non-indigenous fishes that had historically been introduced into the catchments. Although wilderness management policies prohibit the introduction of fish into waters that were uninhabited by fish prior to wilderness designation (except where stocking preceded wilderness designation), replacement of introduced non-indigenous fishes with native trout is possible (Anonymous 2006). Public support for this type of integrated project may be greater because the ethical issues of introducing a fish into previously fishless waters can be avoided. On the other hand, there may be some user groups that value the existing non-indigenous fishery. Because such constituencies can be intransigent, this common response to fish removal projects must be anticipated early in the planning stages.

**Restoration:** Restoration activities include activities focused on the Yellowstone subspecies, habitat, or both. In areas where habitat retains the capacity to support reproducing populations, removal of non-indigenous fishes and reintroduction of Yellowstone cutthroat trout may be warranted. The scope of such activities is limited by the size and complexity of the target drainage, but isolating an appropriately large portion of a basin prior to treatment can be effective (Renner 2005). When isolated populations of Yellowstone cutthroat trout are extirpated following a catastrophic disturbance in small watersheds, reintroduction will be necessary. Efforts to remove fish following severe wildfire and temporarily moving them to a more secure environment (e.g., uninhabited stream or hatchery raceways) may be effective because most deleterious habitat perturbations occur within the first year or two following fire (Gresswell 1999). On the other hand, this is an extreme measure, and efforts to protect the evolutionary capacity of aquatic systems (including native biota) to respond to disturbance, such as fire, is probably a more effective strategy for ensuring the persistence of Yellowstone cutthroat trout.

Because habitat degradation is commonly associated with declines of Yellowstone cutthroat trout populations, habitat improvement has been, and will probably continue to be, critical to the persistence of the subspecies. Concomitantly, approaches to habitat restoration should move beyond standard tactical, site-based activities, toward a more ecologically-based strategy (Frissell 1997) at the watershed scale. Goals of an ecological strategy include (1) maintaining future recovery options by sustaining diverse secure habitats and the native aquatic biota that are supported in these areas; (2) securing existing populations and critical refugia that support historical ecosystem function; and (3) promoting recovery with the greatest probability of improving the status of Yellowstone cutthroat trout by beginning from existing strongholds and incrementally extending the influences of these ecosystem processes.

Perhaps the most critical component of habitat restoration/enhancement relates to the maintenance of natural stream flow and the integrity of the stream network. Throughout the range of the Yellowstone cutthroat trout, water diversion has resulted in substantial dewatering, and climate change will exacerbate this situation. Dewatering and diversion dams have contributed to the fragmentation of stream networks and the subsequent isolation of headwater tributaries and loss of migratory life-history forms (Winters et al. 2004b). Furthermore, entrainment of fish into irrigation ditches at diversion points can be substantial, and screens can be effective for reducing losses (Gale 2005).

Although the specific habitat features that are related to distribution and abundance of salmonids are not thoroughly understood (Ganio et al. 2005, Gresswell et al. 2006), management activities that contribute to the natural integrity of stream networks should be part of all habitat restoration and protection programs. For example, the importance of large woody debris for channel structure and cover is well documented, and management options that protect riparian vegetation have positive effects on stream networks (Gresswell 2005). Grazing management can also be used to protect stream banks and to maintain channel structure in many arid areas within the historical range of the Yellowstone cutthroat trout where livestock grazing is common (Gresswell et al. 1989), and improved management is integral to restoration in areas that have been degraded by poor land-management practices.

## *Information Needs*

In order to understand the natural capacity of the Yellowstone cutthroat trout, it is important to evaluate life-history strategies and organization in areas where the effects of anthropogenic activities can be minimized. Management of Yellowstone cutthroat trout has historically focused on maintaining angler harvest, and as a result, information concerning unperturbed populations is relatively scarce. In many cases, the influence of angler harvest has been neglected in research, even though it can have substantial effects on population structure and abundance (Gresswell et al. 1994, Gresswell and Liss 1995). Although there is a plethora of data from Yellowstone Lake describing Yellowstone cutthroat trout life history during the 1950's, this was a period when the influence of cultured fish and angler harvest was at a maximum. Absence of major anthropogenic habitat perturbation and reduction of angler harvest since the mid-1970's in Yellowstone National Park are major factors that make the Park an ideal area for interpreting natural variation of Yellowstone cutthroat trout.

More specifically, information concerning life-history diversity and its relationship to genetic variation are critical to the protection of the remaining populations of Yellowstone cutthroat trout. Varley and Gresswell (1988) suggested that the greatest threat to the subspecies was the continued decline in genetic variability represented by unique local populations. Although Allendorf and Leary (1988) reported low genetic divergence at isozyme loci of Yellowstone cutthroat trout, they emphasized that it did not imply absence of important genetic differences between populations. Considering efforts to preserve genetic diversity, Echelle (1991) cautioned that no single measure of diversity should take precedence over other forms of information. Identifying differences among populations can provide important information concerning local adaptation and the relationship between life-history organization and specific aspects of habitat. Documentation of life-history differentiation is necessary to provide management support for the protection of unique life-history types in the absence of documented isozyme divergence.

The influence of environment on life history of the Yellowstone cutthroat trout is another area where research is needed. Information about habitat requirements for different ontogenetic stages promotes understanding of the relative effects of numerous anthropogenic activities, and therefore, a thorough understanding of ontogeny and inter- and intrapopulation variation in ontogenetic development is vital. Investigating relationships between life history and habitat in areas where anthropogenic perturbations are minimal can provide insight into current levels of degradation and capacity for restoration. Broad-scale habitat factors that influence distribution, dispersal, and recolonization of Yellowstone cutthroat trout are poorly understood at present; however, this information is crucial for evaluating the effects of current land-use activities and anticipated climate change.

Although population size and age structure is commonly used for monitoring status through time, the use of scales to establish age of Yellowstone cutthroat trout has not been validated (sensu Beamish and McFarlane 1983) beyond age 2. Hubert et al. (1987) reported only 56 percent agreement between ages of Yellowstone cutthroat trout established with scales, otoliths, and dorsal and pectoral fin rays; agreement between readers was also low for all of the structures. Lack of validation, poor concordance among methods, and the difficulty in establishing age at first annulus cast doubt upon reliability of ageing techniques used for Yellowstone cutthroat trout, especially for comparisons among populations and environments. Validation studies are needed for populations from a wide range of environmental settings, both fluvial and lacustrine. Emphasis on accuracy, precision, and development of conversion factors between various techniques should be encouraged.

Research concerning the indirect effects of angling (e.g., redd trampling and bank erosion) may be necessary in areas where angler effort is high. Roberts and White (1992) demonstrated that wading could cause mortality to eggs and fry. The implications of these results may be especially significant when effort increases during the reproductive season. Kelly (1993) found that wading did not significantly affect mortality of eggs and fry in the Yellowstone River (Yellowstone Lake outlet to Upper Falls); current regulations that prohibit angling until July 15 provide protection throughout the area. Angler trails are common in this section of the Yellowstone River and other riparian areas in Yellowstone National Park where angler effort is substantial. Roberts and White (1992) suggest that restricting livestock access to spawning areas may be necessary to achieve maximum benefit from wading restrictions.

Long-term monitoring is integral to understanding interannual variation of Yellowstone cutthroat populations and relationships between habitat and climatic variation. Because monitoring is useful for determining the effects of angler harvest and long-term habitat changes, it is essential that such programs be maintained through time. Large interannual variation and temporal autocorrelation underscore the importance of extending research beyond the common 2 to 3 year period. Much of our understanding about effects of anthropogenic disturbance on populations of Yellowstone cutthroat trout is associated with long-term projects. A robust methodology for selecting monitoring sites is important to insure that inference is valid beyond the individual sample location.

# References

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

Allan, J.D. 1995. Stream ecology: structure and function of running waters. Chapman and Hall, London.

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

Allendorf, F.W., R.F. Leary, N.P. Hitt, K.L. Knudsen, L.L. Lundquist, and P. Spruell. 2004. Intercrosses and the U.S. Endangered Species Act: Should hybridized populations be included as westslope cutthroat trout? Conservation Biology 18:1203-1213.

Andree, K., B.E. MacConnell, and R.P. Hedrick. 2002. A nested polymerase chain reaction for the detection of genomic DNA of *Myxobolus cerebralis* in rainbow trout *Oncorhynchus mykiss*. Diseases of Aquatic Organisms 34:145-154.

Angeler, D.G. and J.M. Moreno. 2007. Zooplankton community resilience after press-type anthropogenic stress in temporary ponds. Ecological Applications 17:1105-1115.

Anonymous. 2000. Memorandum of agreement for conservation and management of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) among Montana, Idaho, Wyoming, Nevada, Utah, U.S. Forest Service, Yellowstone National Park, and Grand Teton National Park. Montana Department of Fish, Wildlife and Parks, Helena, MT.

Anonymous. 2006. Policies and guidelines for fish and wildlife management in National Forest and Bureau of Land Management Wilderness (as amended June 2006). USDA Forest Service, Rocky Mountain Region, Denver, CO.

Armantrout, N.B., compiler. 1998. Glossary of aquatic habitat inventory terminology. American Fisheries Society, Bethesda, MD.

Arnold, B.B. and F.P. Sharpe. 1967. Summary report of lake and stream investigations for 1966, U.S. Fish and Wildlife Service, Yellowstone National Park, WY.

Bagenal, T.B. 1978. Aspects of fish fecundity. Pages 75-101 *in* S.D. Gerking, editor. Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford.

Ball, O.P. 1955. Some aspects of homing in cutthroat trout. Proceedings of the Utah Academy of Science, Arts, and Letters 32:75-80.

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

Bangham, R.V. 1951. Parasites of fish in the upper Snake River drainage and in Yellowstone Lake, WY. Zoologica 36:213-217.

Bartholomew, J.L. and P.W. Reno. 2002. The history and dissemination of whirling disease. Pages 3-24 *in* J.L. Bartholomew and C.J. Wilson, editors. Whirling disease: reviews and current topics. American Fisheries Society, Symposium 29, Bethesda, MD.

Bateman, D.S., R.E. Gresswell, and C.E. Torgersen. 2005. Evaluating single-pass catch as a tool for identifying spatial pattern in fish distribution. Freshwater Ecology 20:335-345.

Bayley, P.B. and J.T. Peterson. 2001. An approach to estimate probability of presence and richness of fish species. Transactions of the American Fisheries Society 130:620-633.

Beamish, R.J. and G.A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112:735-743.

Behnke, R.J. 1988. Phylogeny and classification of cutthroat trout. Pages 1-7 *in* R.E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, MD.

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

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

Belford, D.A. and W.R. Gould. 1989. An evaluation of trout passage through six highway culverts in Montana. Transactions of the American Fisheries Society 9:437-445.

Bender, E.A., T.J. Case, and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65:1-13.

Benson, N.G. 1960. Factors influencing production of immature cutthroat in Arnica Creek, Yellowstone Park. Transactions of the American Fisheries Society 89:168-175.

Benson, N.G. 1961. Limnology of Yellowstone Lake in relation to the cutthroat trout. U.S. Fish and Wildlife Service, Research Report 56, Washington, D.C.

Benson, N.G. and R.V. Bulkley. 1963. Equilibrium yield management of cutthroat trout in Yellowstone Lake. U.S. Fish and Wildlife Service Research Report 62, Washington, D.C.

Berg, R.K. 1975. Fish and game planning, upper Yellowstone and Shields river drainages. Montana Department of Fish, Wildlife and Parks, Federal Aid in Fish Restoration, Project FW-3-R, Job 1-c, Helena, MT.

Bettles, C.M., M.F. Docker, B. Dufour, and D.D. Heath. 2005. Hybridization dynamics between sympatric species of trout: loss of reproductive isolation. Journal of Evolutionary Biology 18:1220-1233.

Bigelow, P. 2008. National Park Service. United State Geological Survey, Bozeman, MT. Personal communication.

Bigelow, P.E., T.M. Koel, D. Mahony, B. Ertel, B. Rowdon, and S.T. Oliff. 2003. Protection of native Yellowstone cutthroat trout in Yellowstone Lake - Yellowstone National Park Wyoming. USDOI/NPS, Technical Report NPS/NRWRD/NRTR-2003/314, Yellowstone National Park, WY.

Binns, N.A. 1977. Present status of indigenous populations of cutthroat trout, *Salmo clarki*, in southwest Wyoming. Wyoming Game and Fish Department, Fisheries Technical Bulletin 2, Cheyenne, WY.

Biodiversity Legal Foundation, Alliance for the Wild Rockies, Montana Ecosystems Defense Council and G. Wuerthner. 1998. Petition for a rule to list the Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) as threatened under the Endangered Species Act, 16 U.S.C. 1531 *et seq*. (1973 as amended). U.S. Fish and Wildlife Service, Washington, D.C.

Bowler, B. 1975. Factors influencing genetic control in lakeward migrations of cutthroat trout fry. Transactions of the American Fisheries Society 104:474-482.

Briggs, J.C. 1955. Behavior pattern in migratory fishes. Science 122:240.

Brown, L.R. and P.B. Moyle. 1997. Invading species in the Eel River, California: successes, failures, and relationships with resident species. Environmental Biology of Fishes 49:271-291.

Brown, R.S. 1999. Fall and early winter movements of cutthroat trout, *Oncorhynchus clarki*, in relation to water temperature and ice conditions in Dutch Creek, Alberta. Environmental Biology of Fishes 55:359-368.

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

Budy, P., G.P. Thiede, and P. McHugh. 2007. Quantification of the vital rates, abundance, and status of a critical, endemic population of Bonneville cutthroat trout. North American Journal of Fisheries Management 27:593-604.

Bulkley, R.V. 1961. Fluctuations in age composition and growth rate of cutthroat trout in Yellowstone Lake. U.S. Fish and Wildlife Service Research Report 54. Washington, D.C.

Burckhardt, J.C. and W.A. Hubert. 2002. The effects of habitat features on whirling disease infection across a Rocky Mountain watershed. Proceedings the 2002 Whirling Disease Symposium.

Byers, J.E. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos 97:449-458.

Byorth, P.A. 1990. An evaluation of Yellowstone cutthroat trout production in three tributaries of the Yellowstone River, Montana. Master's thesis. Montana State University. Bozeman, MT.

Campbell, M.R., J. Dillon, and M.S. Powell. 2002. Hybridization and introgression in a managed, native population of Yellowstone cutthroat trout: genetic detection and management implications. Transactions of the American Fisheries Society 131:364-375.

Carl, L.M. and J.D. Stelfox. 1989. A meristic, morphometric, and electrophoretic analysis of cutthroat, *Salmo clarki*, from two mountain lakes in Alberta. Canadian Field-Naturalist 103:81-85.

Carlander, K.D. 1969. Handbook of freshwater fishery biology, Volume 1. Iowa State University Press, Ames, IA.

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

Clancy, C. Montana Department of Fish, Wildlife and Parks. Personal communication. 1995.

Clancy, C.G. 1988. Effects of dewatering on spawning by Yellowstone cutthroat trout in tributaries to the Yellowstone River, Montana. Pages 37-41 *in* R. E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, MD.

Cohen, W.B., T.A. Spies, R.J. Alig, D.R. Oetter, T.K. Maiersperger, and M. Fiorella. 2002. Characterizing 23 years (1972-95) of stand replacement disturbance in western Oregon forests with LandSAT imagery. Ecosystems 5: 122-137.

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 high-elevation Colorado streams. Transactions of the American Fisheries Society 136:1231-1244.

Colyer, W.T., J.L. Kershner, and R.H. Hilderbrand. 2005. Movements of fluvial Bonneville cutthroat trout in the Thomas Fork of the Bear River, Idaho-Wyoming. North American Journal of Fisheries Management 25:954-963.

Cope, O.B. 1956. Some migration patterns in cutthroat trout. Proceedings of the Utah Academy of Science, Arts, and Letters 33:113-118.

Cope, O.B. 1957a. Races of cutthroat trout in Yellowstone Lake: Contributions to the study of subpopulations of fishes. U.S. Fish and Wildlife Service Special Scientific Report - Fisheries-208.

Cope, O.B. 1957b. The choice of spawning sites by cutthroat trout. Proceedings of the Utah Academy of Science, Arts, and Letters 34:73-79.

Cope, O.B. 1958. Incidence of external parasites on cutthroat trout in Yellowstone Lake. Proceedings of the Utah Academy of Science, Arts, and Letters 35:95-100.

Crait, J. 2005. River otters, cutthroat trout, and their future in Yellowstone National Park. The River Otter Journal 11: 1-3.

Crait, J.R. and M. Ben-David. 2006. River otters in Yellowstone Lake depend on a declining cutthroat population. Journal of Mammalogy 87:485-494.

Cunjak, R.A. and J.M. Green. 1986. Influence of water temperature on behavioral interactions between juvenile brook char, *Salvelinus fontinalis*, and rainbow trout, *Salmo gairdneri*. Canadian Journal of Zoology 64:1288-191.

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

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

Davenport, M.B. 1974. Piscivorous avifauna on Yellowstone Lake, Yellowstone National Park. U.S. National Park Service, Yellowstone National Park, WY.

De Rito, Jr. J.N. 2005. Assessment of reproductive isolation between Yellowstone cutthroat trout and rainbow trout in the Yellowstone River, Montana. Master's thesis. Montana State University, Bozeman, MT.

De Staso III, J. 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.

Dean, J.L. and L.E. Mills. 1971. Fishery Management Investigations, Yellowstone National Park. Bureau of Sport Fisheries and Wildlife, Technical Report for 1970, Yellowstone National Park, WY.

Dean, J.L. and J.D. Varley. 1974. Fishery Management Investigations, Yellowstone National Park. Bureau of Sport Fisheries and Wildlife, Technical Report for 1973, Yellowstone National Park, WY.

Dean, J.L., J.D. Varley, and R.E. Gresswell. 1975. Fishery Management Program, Yellowstone National Park. Bureau of Sport Fisheries and Wildlife, Technical Report for 1974, Yellowstone National Park, WY.

Dill, W.A. and A.J. Cordone. 1997. History and status of introduced fishes in California, 1871-1996: Conclusions. Fisheries (Bethesda) 22(10):15-18, 35.

DuBey, R., C. Caldwell, and W.R. Gould. 2005. Effects of temperature, photoperiod, and *Myxobolus cerebralis* infection on growth, reproduction, and survival of *Tubifex tubifex* lineages. Journal of Aquatic Animal Health 17:338-344.

Dunham, J.B., G.L. Vinyard, and B.E. Rieman. 1997. Habitat fragmentation and extinction risk of Lahontan cutthroat trout. North American Journal of Fisheries Management 17:1126-1133.

Dunham, J.B., M.K. Young, R.E. Gresswell, and B.E. Rieman. 2003. Effects of fire on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions. Forest Ecology and Management 178: 183-196.

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

Dwyer, W.P. and R.H. Kramer. 1975. The influence of temperature on scope for activity in cutthroat trout, *Salmo clarki*. Transactions of the American Fisheries Society 104:522-554.

Dwyer, W.P. and C.E. Smith. 1989. Metacercariae of *Diplostomum spathaceum* in the eyes of fishes from Yellowstone Lake, Wyoming. Journal of Wildlife Diseases 25:126-129.

Ebersole, J.L., W.J. Liss, and C.A. Frissell. 1996. Restoration of stream habitats in managed landscapes in the western USA: restoration as re-expression of habitat capacity. Environmental Management 21:1-14.

Echelle, A.A. 1991. Conservation genetics and genetic diversity in freshwater fishes of western North American battle against extinction: native fish management in the American West. Pages 141-153 *in* M.L. Minckley and J.E. Deacon, editors. Battle against extinction: native fish management in the American West. The University of Arizona Press, Tucson, AZ.

Elle, S. and M. Gamblin. 1993. Region 6 (Idaho Falls) rivers and streams investigation. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project F-71-R-15, Job 6(IF)-c, Job Progress Report, Boise, ID.

Farag, A.M., D. Skaar, D.A. Ninick, E. MacConnell, and C. Hogstrand. 2003. Characterizing aquatic health using salmonid mortality, physiology, and biomass estimates in streams with elevated concentrations of arsenic, cadmium, copper, lead, and zinc in the Boulder River watershed, Montana. Transactions of the American Fisheries Society 132:450-467.

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., S. Nakano, and S. Kitanoc. 1997. Experimentally induced foraging mode shift by sympatric charrs in a Japanese mountain stream. Behavioral Ecology 8:414-420.

Fausch, K.D., B.E. Rieman, M.K. Young, and J.B. Dunham. 2006. Strategies for conserving native salmonid populations at risk from nonnative fish invasions: tradeoffs in using barriers to upstream movement. General Technical Report RMRS-GTR-174, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Felicetti, L.A., C.C. Schwartz, R.O. Rye, K.A. Gunther, J.G. Crock, M.A. Haroldson, L. Waits, and C.T. Robbins. 2004. Use of naturally occurring mercury to determine the importance of cutthroat trout to Yellowstone grizzly bears. Canadian Journal of Zoology 82:493-501.

Ferguson, M.M., R.G. Danzmann, and F.W. Allendorf. 1985. Absence of developmental incompatibility in hybrids between rainbow trout and two subspecies of cutthroat trout. Biochemical Genetics 23:557-570.

Finlayson, B., W. Somer, D. Duffield, D. Propst, C. Mellison, T. Pettengill, H. Sexauer, T. Nesler, S. Gurtin, J. Elliot, F. Partridge, and D. Skaar. 2005. Native inland trout restoration on national forests in the western United States: time for improvement. Fisheries (Bethesda) 30(5):10-19.

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

Frissell, C.A. 1997. Ecological principles. Pages 96-115 *in* J.E. Williams, C.A. Wood, and M.P. Dombeck, editors. Watershed restoration: principles and practices. American Fisheries Society, Bethesda, MD.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199-214.

Frissell, C.A., W.J. Liss, R.E. Gresswell, R.K. Nawa, and J.L. Ebersole. 1997. A resource in crisis: changing the measure of salmon management: Pacific salmon and their ecosystems: status and future options. Pages 411-444 *in* D.J. Stouder, P.A. Bisson, and R.J. Naiman, editors. Chapman and Hall, New York, NY.

Gale, S.B. 2005. Entrainment losses of westslope cutthroat trout into screened and unscreened irrigation canals on Skalkaho Creek, Montana. Master’s thesis. Montana State University, Bozeman, MT.

Ganio, L.M., C.E. Torgersen, and R.E. Gresswell. 2005. Describing spatial pattern in stream networks: a practical approach. Frontiers in Ecology and the Environment 3:138-144.

Gerking, S.D. 1959. The restricted movement of fish populations. Biological Review 34:221-242.

Gresswell, R.E. 1986. Special regulations as a fishery management tool in Yellowstone National Park: Fisheries and coastal wetlands. Pages 119-126 *in* G. Larson and M. Soukup, editors. Status and Management of Interior Stocks of Cutthroat Trout .George Wright Society and U.S. National Park Service, Fort Collins, CO.

Gresswell, R.E. 1991. Use of antimycin for removal of brook trout from a tributary of Yellowstone Lake. Transactions of the American Fisheries Society 11:83-90.

Gresswell, R.E. 1995. Yellowstone cutthroat trout. Pages 36-54 *in* M. Young, editor. Conservation assessment for inland cutthroat trout. General Technical Report RM-GTR-256, USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Gresswell, R.E. 1997. Introduction to ecology and management of potamodromous salmonids. North American Journal of Fisheries Management 17:1027-1028.

Gresswell, R.E. 1999. Fire and aquatic ecosystems in forested biomes of North America. Transactions of the American Fisheries Society 128:193-221.

Gresswell, R.E. 2005. Forestry practices and aquatic biodiversity: fish. Pages 18-23 *in* D. Sarr, D. Odion, D. Hibbs, J. Weikel, R. Gresswell, R. Bury, N. Czarnomski, R. Pabst, J. Shatford, and A. Moldenke, editors. Riparian zone forest management and the protection of biodiversity: A problem analysis. Technical Bulletin No. 908, National Center for Air and Stream Improvement (NCASI), Inc., Research Triangle Park, NC.

Gresswell, R.E. and R. D. Harding. 1997. The role of special angling regulations in management of coastal cutthroat trout. Pages 151-156 *in* J.D. Hall, P.A. Bisson, and R.E. Gresswell, editors. Sea-run cutthroat trout: biology, management, and future conservation. Oregon Chapter, American Fisheries Society, Corvallis, OR.

Gresswell, R.E. and S.R. Hendricks. 2007. Population-scale movement of coastal cutthroat trout in a naturally isolated stream network. Transactions of the American Fisheries Society 136:238-253.

Gresswell, R.E. and W.J. Liss. 1995. Values associated with management of Yellowstone cutthroat trout in Yellowstone National Park. Conservation Biology 9:159-165.

Gresswell, R.E. and J.D. Varley. 1988. Effects of a century of human influence on the cutthroat trout of Yellowstone Lake. Pages 45-52 *in* R.E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, MD.

Gresswell, R.E., B.A. Barton, and J.L. Kershner. 1989. Practical approaches to riparian resource management. U.S. Bureau of Land Management, Billings, MT.

Gresswell, R.E., W.J. Liss, and G.L. Larson. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 51 (Supplement 1):298-309.

Gresswell, R.E., D.S. Bateman, G.W. Lienkaemper, and T.J. Guy. 2004. Geospatial techniques for developing a sampling frame of watersheds across a region. Pages 517-53 *in* T. Nishida, P.J. Kailola, and C.E. Hollingworth, editors. GIS/spatial analyses in fishery and aquatic sciences (Vol. 2). Fishery-Aquatic GIS Research Group, Saitama, Japan.

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

Gresswell, R.E., W.J. Liss, G. Lomnicky, E.A. Deimling, R.L. Hoffman, and T. Tyler. 1997b. Using mark-recapture methods to estimate fish abundance in small mountain lakes. Northwest Science 79:31-44.

Gresswell, R.E., C.E. Torgersen, D.S. Bateman , T.J. Guy, S.R. Hendricks, and J.E.B. Wofford. 2006. A spatially explicit approach for evaluating relationships among coastal cutthroat trout, habitat, and disturbance in headwater streams. Pages 457-471 *in* R. Hughes, L. Wang, and P. Seelbach, editors. Influences of landscapes on stream habitats and biological assemblages. American Fisheries Society, Bethesda, MD.

Griffith, J.S. and R.W. Smith. 1993. Use of winter concealment cover by juvenile cutthroat and brown trout in the South Fork of the Snake River. North American Journal of Fisheries Management 13:823-830.

Griffith, Jr., J.S. 1988. Review of competition between cutthroat trout and other salmonids. Pages 134-140 *in* R.E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, MD.

Guy, T.J., R.E. Gresswell, and M.A. Banks. 2008. Landscape-scale evaluation of genetic structure among barrier-isolated populations of coastal cutthroat trout, *Oncorhynchus clarkii clarkii*. Canadian Journal of Fisheries and Aquatic Sciences 65:1749-1762.

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

Hall, M.C. 1930. Report on parasites of pelican and trout, investigations at Yellowstone Lake, 1930. Report to the U.S. National Park Service, Yellowstone National Park, WY.

Hall, Jr., R.O., J.L. Tank, and M.F. Dydbahl. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. Frontiers in Ecology and the Environment 1:407-411.

Hankin, D.G. and G.H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45:834-844.

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

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

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

Haroldson, M., K.A. Gunther, Reinhart, D.P., S.R. Podruzny, C. Cegelski, L. Waits, T. Wyman, and J. Smith. 2005. Changing numbers of spawning cutthroat trout in tributary streams of Yellowstone Lake and estimates of grizzly bears visiting streams from DNA. Ursus 16:167-180.

Harper, D.D. and A.M. Farag. 2004. Winter habitat use by cutthroat trout in the Snake River near Jackson, Wyoming. Transactions of the American Fisheries Society 133:15-25.

Hayden, P.S. 1967. The reproductive behavior of the Snake River cutthroat in three tributary streams in Wyoming. Wyoming Game and Fish Department, Cooperative Research Project 4, Cheyenne, WY.

Heckmann, R. 1971. Parasites of cutthroat trout from Yellowstone Lake, Wyoming. Progressive Fish-Culturist 33: 103-106.

Heckmann, R.A. and H.L. Ching. 1987. Parasites of the cutthroat trout, *Salmo clarki*, and longnose suckers, *Catostomus catostomus*, from Yellowstone Lake, Wyoming. Great Basin Naturalist 47:259-275.

Hedrick, R. P., T. S. McDowell, K. Mukkatira, M. P. Georgiadis, and E. MacConnell. 1999. Susceptibility of selected inland salmonids to experimental induced infections with *Myxobolus cerebralis* the causative agent of whirling disease. Journal of Aquatic Animal Health 11:330-339.

Henderson, R., J. L. Kershner, and C.A. Toline. 2000. Timing and location of spawning by nonnative wild rainbow trout and native cutthroat trout in the South Fork Snake River, Idaho, with implications. North American Journal of Fisheries Management 20:584-596.

Hilborn, R. and M. Mangel. 1997. The ecological detective: confronting models with data. Monographs in Population Biology 28, Princeton University Press, Princeton, NJ.

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

Hilderbrand, R.H. and J.L. Kershner. 2000a. Movement patterns of stream-resident cutthroat trout in Beaver Creek, Idaho-Utah. Transactions of the American Fisheries Society 129:1160-1170.

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

Hiner, M. and C.M. Moffitt. 2001. Variation in infections of *Myxobolus cerebralis* in field-exposed cutthroat and rainbow trout in Idaho. Journal of Aquatic Animal Health 13:124-132.

Hitt, N.P., C.A. Frissell, C.C. Muhlfeld, and F.W. Allendorf. 2003. Spread of hybridization between native westslope cutthroat trout, *Oncorhynchus clarki lewisi*, and nonnative rainbow trout, *Oncorhynchus mykiss*. Canadian Journal of Fisheries and Aquatic Sciences 60:1440-1451.

Hoffman, G.L. 1967. Parasites of North American freshwater fishes. University of California Press, Berkeley, CA.

Hubert, W.A., G. Baxter, and M. Harrington. 1987. Comparison of age determinations based on scales, otoliths and fin rays for cutthroat trout from Yellowstone Lake. Northwest Science 61:32-36.

Idaho Department of Fish and Game. 2007. Management plan for conservation of Yellowstone cutthroat trout in Idaho. Idaho Department of Fish and Game, Boise, ID.

Imhof, J.G., J. Fitzgibbon, and W.K. Annable. 1996. A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. Canadian Journal of Fisheries and Aquatic Sciences 53 (Supplement 1):312-326.

Intergovernmental Panel on Climate Change and WG I and WGII. 2001. Climate change 2001. Cambridge University Press, Cambridge.

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

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.

Isaak, D.J. and W.A. Hubert. 2004. Nonlinear response of trout abundance to summer stream temperatures across a thermally diverse montane landscape. Transactions of the American Fisheries Society 133:1254-1259.

Jager, H.I., W. Van Winkle, and B.D. Holcomb. 1999. Would hydrologic climate changes in Sierra Nevada streams influence trout persistence? Transactions of the American Fisheries Society 128:222-240.

Jahn, L.A. 1969. Movements and homing of the cutthroat trout (*Salmo clarki*) from open-water areas of Yellowstone Lake. Journal of the Fisheries Research Board of Canada 26:1243-1261.

Janetski, D.J. 2006. Genetic considerations for the conservation and management of Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) in Yellowstone National Park. Master's thesis. Brigham Young University, Provo, UT.

Johnson, J.E. 1987. Protected fishes of the United States and Canada. American Fisheries Society, Bethesda, MD.

Johnson, R.L. 1964. Stream channel alteration inventory - Shields River. Montana Department of Fish, Wildlife, and Parks, Federal Aid in Fish Restoration, Project F-9-R-12, Job 2, Job Progress Report, Helena, MT.

Jones, R.D., R. Andrascik, D.G. Carty, R.E. Gresswell, D.L. Mahony, and S. Relya. 1990. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report for 1989, Yellowstone National Park, WY.

Jones, R.D., R. Andrascik, D.G. Carty, L.R. Kaeding, B.M. Kelly, D.L. Mahony, and T. Olliff. 1992. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report for 1991, Yellowstone National Park, WY.

Jones, R.D., P.E. Bigelow, R.E. Gresswell, and R.A. Valdez. 1982. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report for 1981, Yellowstone National Park, WY.

Jones, R.D., D.G. Carty, R.E. Gresswell, K.A. Gunther, L.D. Lentsch, and J. Mohrman. 1985. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report for 1984, Yellowstone National Park, WY.

Jones, R.D., D.G. Carty, R.E. Gresswell, C.J. Hudson, L.D. Lentsch, and D.L. Mahony. 1986. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report for 1985, Yellowstone National Park, WY.

Jones, R.D., R.E. Gresswell, S.M. Rubrecht, P.E. Bigelow, and D. Carty. 1981. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report for 1980, Yellowstone National Park, WY.

Jones, R.D., J.D. Varley, D.E. Jennings, S.M. Rubrecht, and R.E. Gresswell. 1979. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report for 1978, Yellowstone National Park, WY.

Jordan, D.S. 1891. A reconnaissance of streams and lakes of Yellowstone National Park, Wyoming in the interest of the U.S. Fish Commission. Bulletin of the U.S. Fish Commission 9:41-63.

Kaeding, L.R. 2002. Factors influencing the distribution of American white pelicans foraging on the Yellowstone River, Yellowstone National Park, USA. Waterbirds 25:305-311.

Kaeding, L.R., G.D. Boltz, and D.G. Carty. 1996. Lake trout discovered in Yellowstone Lake threaten native cutthroat trout. Fisheries (Bethesda) 21(3):16-20.

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

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.

Kelly, B.M. 1993. Ecology of Yellowstone cutthroat trout and evaluation of potential effects of angler wading in the Yellowstone River. Master's thesis. Montana State University. Bozeman, MT.

Kerans, B.L., R.I. Stevens, and J.C. Lemmon. 2005a. Water temperature affects host-parasite interaction: *Tubifex tubifex* and *Myxobolus cerebralis*. Journal of Aquatic Animal Health 17:216-221.

Kerans, B.L., M.F. Dybdahl, M.M. Gangloff, and J.E. Jannot. 2005b. *Potamopyrgus antipodarum*: distribution, density, and effects on native macroinvertebrate assemblages in the Greater Yellowstone Ecosystem. Journal of the North American Benthological Society 24:123-138.

Kershner, J. 2006. Center Director, Northern Rocky Mountain Science Center, United States Geological Survey, Bozeman, MT. Personal communication.

Kiefling, J.W. 1978. Studies on the ecology of the Snake River cutthroat trout. Fisheries Technical Bulletin No. 3, Wyoming Game and Fish Department, Cheyenne, WY.

Koel, T.M., P.E. Bigelow, P.D. Doepke, B.D. Ertel, and D.L. Mahony. 2005. Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. Fisheries (Bethesda) 30:10-19.

Koel, T.M., J.L. Arnold, P.E. Bigelow, P.D. Doepke, B.D. Ertel, and D.L. Mahony. 2004. Yellowstone Fisheries and Aquatic Sciences, Annual Report 2003. National Park Service, Center for Resources, Yellowstone National Park, Wyoming, YCR 2004-03.

Koel, T.M., J.L. Arnold, P.E. Bigelow, P.D. Doepke, B.D. Ertel, and M.E. Ruhl. 2007. Yellowstone Fisheries and Aquatic Sciences, Annual Report 2006. National Park Service, Center for Resources, Yellowstone National Park, Wyoming, YCR 2007-04.

Koel, T.M., D.L. Mahony, K.L. Kinnan, C. Rasmussen, C.J. Hudson, S. Murcia, and B.L. Kerans. 2006. *Myxobolus cerebralis* in native cutthroat trout of the Yellowstone Lake ecosystem. Journal of Aquatic Animal Health 18: 157-175.

Kruse, C.G., W.A. Hubert, and F.J. Rahel. 1997. Geomorphic influences on the distribution of Yellowstone cutthroat trout in the Absaroka Mountains, Wyoming. Transactions of the American Fisheries Society 126:418-427.

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

Kruse, C.G., W.A. Hubert, and F.J. Rahel. 2001. An assessment of headwater isolation as a conservation strategy for cutthroat trout in the Absaroka Mountains of Wyoming. Northwest Science 75:1-11.

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.

LaBar, G.W. 1971. Movement and homing of cutthroat trout (*Salmo clarki*) in Clear and Bridge creeks, Yellowstone National Park. Transactions of the American Fisheries Society 100:41-49.

Lake, P.S. 2000. Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society 19:573-592.

Lake, P.S. 2003. Ecological effects of perturbation by drought in flowing waters. Freshwater Biology 48:1161-1172.

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

Larsen, D.P., P.R. Kaufmann, T.M. Kincaid, and N.S. Urquhart. 2004. Detecting persistent change in the habitat of salmon-bearing streams in the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 61:283-291.

Larson, G.L., S.E. Moore, and B. Carter. 1995. Ebb and flow of encroachment by nonnative rainbow trout in a small stream in the southern Appalachian Mountains. Transactions of the American Fisheries Society 124:613-622.

Leary, R.F., F.W. Allendorf, and K.L. Knudsen. 1989. Genetic divergence among Yellowstone cutthroat trout populations in the Yellowstone River drainage, Montana: update. University of Montana, Division of Biological Sciences, Population Genetics Laboratory Report, Missoula, MT.

Leary, R.F., F.W. Allendorf, S.R. Phelps, and K.L. Knudsen. 1987. Genetic divergence and identification of seven cutthroat trout subspecies and rainbow trout. Transactions of the American Fisheries Society 116:580-587.

Leary, R.F., F.W. Allendorf, and G.K. Sage. 1995. Hybridization and introgression between introduced and native fish. Pages 91-101 *in* H.L. Schramm, Jr. and R.G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society, Symposium 15, Bethesda, MD.

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.

Linton, E. 1891. A contribution to the life history of *Dibothrium cordiceps*, a parasite infesting the trout of Yellowstone Lake. Bulletin of the United States Fish Commission 4:337-358.

Loudenslager, E. J. and G.A.E. Gall. 1980. Geographic patterns of protein variation and subspeciation in cutthroat trout, *Salmo clarki*. Systematic Zoology 29:27-42.

Loudenslager, E.J. and R.M. Kitchin. 1979. Genetic similarity of two forms of cutthroat trout, *Salmo clarkii*, in Wyoming. Copeia 1979:673-678.

MacConnell, E. and J.E. Peterson. 1991. Proliferative kidney disease in feral cutthroat trout from a remote Montana reservoir: a first case. Journal of Aquatic Animal Health 4:182-187.

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

Marnell, L.F., R.J. Behnke, and F.W. Allendorf. 1987. Genetic identification of cutthroat trout, *Salmo clarki*, in Glacier National Park, Montana. Canadian Journal of Fisheries and Aquatic Sciences 44:1830-1839.

Marrin, D.L. and D.C. Erman. 1982. Evidence against competition between trout and nongame fishes in Stampede Reservoir, California. North American Journal of Fisheries Management 2:262-269.

Mattson, D.J. and D.P. Reinhart. 1995. Influences of cutthroat trout (*Oncorhynchus clarki*) on behavior and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975–1989. Canadian Journal of Zoology 73:2072-2079.

May, B.E. 1996. Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*). Pages 11-34 *in* D.A. Duff, editor. Conservation assessment for inland cutthroat trout. USDA Forest Service, Intermountain Region Report, Ogden, UT.

May, B.E. and S.E. Albeke. 2005. Range-wide status of Bonneville cutthroat trout (*Oncorhynchus clarki utah*):2004. Utah Department of Wildlife Resources, Printed Agency Report. Salt Lake City, UT.

May, B.E., S.E. Albeke, and T. Horton. 2007. Range-wide status of Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*): 2006. Montana Department of Fish, Wildlife and Parks, Helena, MT.

May, B.E., W. Urie, and B.B. Shepard. 2003. Range-wide status of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) 2001. Montana Department of Fish, Wildlife and Parks, Helena, MT.

McCleave, J.D. 1967. Homing and orientation of cutthroat trout (*Salmo clarki*) in Yellowstone Lake, with special reference to olfaction and vision. Journal of the Fisheries Research Board of Canada 24:2011-2044.

McEneaney, T. 2002. Piscivorous birds of Yellowstone Lake: their history, ecology, and status. Pages 121-134 *in* R.J. Anderson and D. Harmon, editors. Yellowstone Lake: hotbed of chaos or reservoir of resilience? Proceedings of the 6th Biennial Scientific Conference on the Greater Yellowstone Ecosystem. Yellowstone Center for Resources and the George Wright Society, Yellowstone National Park, WY and Hancock, MI.

Mealey, S.P. 1980. The natural food habits of grizzly bears in Yellowstone National Park, 1973-1974. International Conference on Bear Research and Management 3:281-292.

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

Meronek, T.G., P.M. Bouchard, E.R. Buckner, T.M. Burri, K.K. Demmerly, D.C. Hatleli, R.A. Klumb, S.H. Schmidt, and D.W. Coble. 1996. A review of fish control projects. North American Journal of Fisheries Management 16: 63-74.

Meyer, K. Idaho Department of Fish and Game. Personal communication. 2008.

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

Meyer, K.A., D.J. Schill, F.S. Elle, and W.C. Schrader. 2003a. A long-term comparison of Yellowstone cutthroat trout abundance and size structure in the historical range in Idaho. North American Journal of Fisheries Management 23:149-162.

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

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

Mills, L.E. 1966. Environmental factors and egg mortality of cutthroat trout (*Salmo clarki*) in three tributaries of Yellowstone Lake. Master's thesis. Colorado State University, Fort Collins, CO.

Montana Department of Fish, Wildlife, and Parks. 2000. Cooperative conservation agreement for Yellowstone cutthroat trout within Montana between the Crow Tribe, Montana Department of Fish, Wildlife and Parks, Montana Department of Environmental Quality, Montana Department of Natural Resources and Conservation, USDA-Forest Service, Northern Region, Gallatin and Custer National Forests, USDI-Bureau of Land Management - Montana, USDI-Fish and Wildlife Service, USDI-Bureau of Indian Affairs, Yellowstone National Park . Montana Department of Fish, Wildlife, and Parks, Helena, MT.

Montgomery, M.R. 1995. Many rivers to cross - of good running water, native trout, and the remains of wilderness. Simon and Schuster, New York, NY.

Moore, V. and D. Schill. 1984. South Fork Snake River fisheries inventory. River and stream investigations. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project F-73-R-5, Job Completion Report, Boise, ID.

Moyle, P.B. and B. Vondracek. 1985. Persistence and structure of the fish assemblage in a small California stream. Ecology 66:1-13.

Munro, A.R., T.E. McMahon, and J.R. Ruzycki. 2005. Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 62:79-87.

Nelson, J.S., E.J. Crossman, H. Espinosa-Pérez, L.T. Findley, C.R. Gilbert, R.N. Lea , and J.D. Williams. 2004. Common and scientific names of fishes from the United States, Canada, and Mexico, 6th edition. American Fisheries Society Special Publication 29. Bethesda, MD.

Nico, L.G. and P.L. Fuller. 1999. Spatial and temporal patterns of nonindigenous fish introductions in the United States. Fisheries 24(1):16-27.

Northcote, T.G. 1992. Protection and assessment of potential effects of global environmental change on freshwater sport fish habitat in British Columbia. Geo Journal 28(1):39-49.

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

Novak, M.A., J.L. Kershner, and K.E. Mock. 2005. Molecular genetic investigation of Yellowstone cutthroat trout and finespotted Snake River cutthroat trout. A report in partial fulfillment of Agreement # 165/04 for the State of Wyoming, Wyoming Game and Fish Commission. Utah State University, Logan, UT.

Olsen, A.R., J.E.D. Sedransk, C.A. Gotway, W. Liggett, S. Rathbun, K.H. Reckhow, and L.J. Young. 1999. Statistical issues for monitoring ecological and natural resources in the United States. Environmental Monitoring and Assessment 54:1-45.

Ostberg, C.O. and R.J. Rodriguez. 2002. Novel molecular markers differentiate *Oncorhynchus mykiss* (rainbow trout and steelhead) and *O. clarki* (cutthroat trout) subspecies. Molecular Ecology Notes 2:197-202.

Otto, T.N. and R.A. Heckmann. 1984. Host tissue response for trout infected with Diphyllobothrium cordiceps larvae. Great Basin Naturalist 44:125-132.

Oviatt, C.G., D.R. Currey, and D. Sack. 1992. Radiocarbon chronology of Lake Bonneville, eastern Great Basin, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 99:225-241.

Peterson, D.P. and K.D. Fausch. 2003a. 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. and K.D. Fausch. 2003b. 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., K.D. Fausch, and G.C. White. 2004. Population ecology of an invasion: effects of brook trout on native cutthroat trout. Ecological Applications 14:754-772.

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 trout 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.

Platt, J.R. 1964. Strong inference. Science 146:347-353.

Platts, W.S. 1991. Livestock grazing. American Fisheries Society Special Publication 19:139-179.

Poole, G.C., C.A. Frissell, and S.C. Ralph. 1997. In-stream habitat unit classification: inadequacies for monitoring and some consequences for management. Journal of the American Water Resources Association 33:879-896.

Post, G. 1971. The Diphyllobothrium Cestode in Yellowstone Lake, Wyoming. Agricultural Experiment Station, Research Journal 41, University of Wyoming, Laramie, WY.

Quist, M.C. and W.A. Hubert. 2004. Bioinvasive species and the preservation of cutthroat trout in the western United States: ecological, social, and economic issues. Environmental Science and Policy 7:303-313.

Quist, M.C. and W.A. Hubert. 2005. Relative effects of biotic and abiotic process: a test of the biotic-abiotic constraining hypothesis as applied to cutthroat trout. Transactions of the American Fisheries Society 134:676-686.

Rahel, F.J. 1997. From Johnny Appleseed to Dr. Frankenstein: Changing values and the legacy of fisheries management. Fisheries (Bethesda) 22(8):8-9.

Rahel, F.J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology and Systematics 33:291-315.

Raleigh, R.F. and D.W. Chapman. 1971. Genetic control in lakeward migration of cutthroat trout fry. Transactions of the American Fisheries Society 100:33-40.

Reeves, G.H., F.H. Everest, and J.D. Hall. 1987. Interactions between the redside shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in western Oregon: the influence of water temperature. Canadian Journal of Fisheries and Aquatic Sciences 44:1603-1613.

Reinhart, D.P. and D.J. Mattson. 1990. Bear use of cutthroat trout spawning streams in Yellowstone National Park. International Conference on Bear Research and Management 8:343-350.

Reinhart, D.P., M.A. Haroldson, D.J. Mattson, and K.A. Gunther. 2001. Effects of exotic species on Yellowstone's grizzly bears. Western North American Naturalist 61:277-288.

Renner, D. 2005. Distribution and habitat use by bull trout following the removal of nonnative brook trout. Master's thesis. Oregon State University, Corvallis, OR.

Richardson, J.S. and R.J. Danehy. 2007. A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. Forest Science 53:131-147.

Richmond, G.M. and K.L. Pierce. 1972. Surficial geologic map of the Eagle Peak quadrangle, Yellowstone National Park, Wyoming. U.S. Geological Survey Miscellaneous Geologic Investigations, Map I-637, Washington, D.C.

Rinne, J.N. 1996. Short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. North American Journal of Fisheries Management 16:653-658.

Rinne, J.N. and P.R. Turner. 1991. Reclamation and alteration as management techniques, and a review of methodology in stream renovation Pages 219-244 *in* W.L. Minckley and J.E. Deacon, editors. Battle against extinction: native fish management in the American West. The University of Arizona Press, Tucson, AZ.

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

Roelke, D., S. Augustine, and Y. Buyukates. 2003. Fundamental predictability in multispecies competition: the influence of large disturbance. The American Naturalist 162:615-623.

Romero, N.R., R.E. Gresswell, and J. Li. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. Canadian Journal of Fisheries and Aquatic Sciences 62:1797-1807.

Ruzycki, J.R., D.A. Beauchamp, and D.L. Yule. 2003. Effects on introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13:23-37.

Ryce, E.K.N., A.V. Zale, E. MacConnell, and M. Nelson. 2005. Effects of fish age versus size on the development of whirling disease in rainbow trout. Diseases of Aquatic Organisms 63:69-76.

Schill, D.J. and J.S. Griffith. 1984. Use of Underwater Observations to Estimate Cutthroat Trout Abundance in the Yellowstone River. North American Journal of Fisheries Management 4:479-487.

Schill, D.J., J.S. Griffith, and R.E. Gresswell. 1986. Hooking mortality of cutthroat trout in a catch and release segment of the Yellowstone River, Yellowstone National Park. North American Journal of Fisheries Management 6:226-232.

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

Schrank, A.J., F.J. Rahel, and H.C. Johnstone. 2003. Evaluating laboratory-derived thermal criteria in the field: an example involving Bonneville cutthroat trout. Transactions of the American Fisheries Society 132:100-109.

Schullery, P. and J.D. Varley. 1995. Cutthroat trout and the Yellowstone Lake ecosystem. Pages 12-21 *in* J.D. Varley and P. Schullery, editors. The Yellowstone Lake crisis: confronting a lake trout invasion. U.S. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, WY.

Schumm, S.A. 1956. Evolution of drainage systems and slopes in badlands at Perth Amboy, New Jersey. Bulletin of the Geological Society of America 67:597-646.

Sestrich, C.M. 2005. Changes in native and nonnative fish assemblages and habitat following wildfire in the Bitterroot River Basin, Montana. Master's thesis. Montana State University, Bozeman, MT.

Shepard, B.B. 1992. Fisheries of the upper Yellowstone River including tributary recruitment: Report for years 1989, 1990, and 1991. Montana Department of Fish, Wildlife and Parks, Federal Aid in Fish Restoration, Project F-46-R-2, 3, and 4, Job I-f, Job Progress Report, Helena, MT.

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

Shepard, B.B. and B. Snyder. 2005. Yellowstone cutthroat trout status update for Montana: 2005. Montana Department of Fish, Wildlife, and Parks, Helena, MT.

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

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

Shiozawa, D.K. and R.N. Williams. 1992. Geographic variation, isolation, and evolution of cutthroat trout (*Salmo clarki*). Final Report to the National Geographic Society, Brigham Young University, Provo, UT.

Shreve, R.L. 1969. Stream lengths and basin areas in topologically random channel networks. Journal of Geology 77: 397-414.

Skinner, W.D. 1985. Size selection of food by cutthroat trout (*Salmo clarki*) in an Idaho stream. Great Basin Naturalist 45:327-331.

Smith, G.R. and R.F. Stearley. 1989. The classification and scientific names of rainbow and cutthroat trouts. Fisheries (Bethesda) 14(1):4-10.

Smith, G.R., T.E. Dowling, K.W. Gobalet, T. Lugaski, D.K. Shiozawa, and R.P. Evans. 2002. Biogeography and timing of evolutionary events among Great Basin fishes. Pages 175-234 *in* R. Hershler, D.B. Madsen, and D.R. Currey, editors. Great Basin aquatic systems history. Smithsonian Contributions to the Earth Sciences Number 33, Washington, D.C.

Smith, H.M. and W.C. Kendall. 1921. Fishes of the Yellowstone National Park. Department of Commerce. Bureau of Fisheries Document Number 904, Washington, D.C.

Stapp, P. and G.D. Hayward. 2002a. Effects of an introduced piscivore on native trout: Insights from a demographic model. Biological Invasions 4:299-316.

Stapp, P. and G.D. Hayward. 2002b. Estimates of predator consumption of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. Journal of Freshwater Ecology 17:319-329.

Stearley, R.F. 1992. Historical ecology of Salmoninae, with special reference to *Oncorhynchus*. Pages 622-658 *in* R.L. Mayden, editor. Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford, CA.

Stearley, R.F. and G.R. Smith. 1993. Phylogeny of the Pacific trouts and salmons (*Oncorhynchus*) and genera of the family Salmonidae. Transactions of the American Fisheries Society 122:1-33.

Stefan, H.G., X. Fang, and J.G. Eaton. 2001. Simulated fish habitat changes in North American lakes in response to projected climate warming. Transactions of the American Fisheries Society 130:459-477.

Stevens, D.L. and A.R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262-278.

Strange, R.J. and J.W. Habera. 1998. No net loss of brook trout distributions in areas of sympatry with rainbow trout in Tennessee streams. Transactions of the American Fisheries Society 127:434-449.

Swenson, J.E. 1978. Prey and foraging behavior of ospreys on Yellowstone Lake, Wyoming. Journal of Wildlife Management 42:87-90.

Swenson, J.E., K.L. Alt, and R.L. Eng. 1986. Ecology of bald eagles in the Greater Yellowstone Ecosystem. Wildlife Monographs 95:1-46.

Thompson, P.D. and F.J. Rahel. 1998. Evaluation of artificial barriers in small Rocky Mountain streams for preventing the upstream movement of brook trout. North American Journal of Fisheries Management 18:206-210.

Thorpe, J.E. 1994. Salmonid flexibility: responses to environmental extremes. Transactions of the American Fisheries Society 123:606-612.

Thurow, R.F. 1982. Blackfoot River fishery investigations. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project F-73-r-3, Job Completion Report, Boise, ID.

Thurow, R.F., C.E. Corsi, and V.K. Moore. 1988. Status, ecology, and management of Yellowstone cutthroat trout in Upper Snake River Drainage, Idaho. Pages 25-36 *in* R.E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, MD.

Thurow, R.F. and J.G. King. 1994. Attributes of Yellowstone cutthroat trout redds in a tributary of the Snake River, Idaho. Transactions of the American Fisheries Society 123:37-50.

Thurow, R.F., D.C. Lee, and B.E. Rieman. 1997. Distribution and status of seven native salmonids in the interior Columbia basin and portions of the Klamath River and Great Basins. North American Journal of Fisheries Management 17:1094-1110.

Trombulak, S.C. and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 20:18-30.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, MA.

Utah Division of Wildlife Resources. 2000. Cutthroat trout management: A position paper genetic considerations associated with cutthroat trout management. Publication Number 00-26, Utah Division of Wildlife Resources, Salt Lake City, UT.

Urquhart, N.S., S.G. Paulsen, and D.P. Larsen. 1998. Monitoring for policy-relevant regional trends over time. Ecological Applications 8:246-257.

USDA Forest Service. 2005. Bighorn National Forest revised land and resource management plan. Rocky Mountain Region, Denver, CO.

U.S. Fish and Wildlife Service. 2001. Endangered and threatened wildlife and plants: 90-day finding for a petition to list the Yellowstone cutthroat trout as threatened. Federal Register Volume 66:1244-11249.

U.S. Fish and Wildlife Service. 2006. Endangered and threatened wildlife and plants: 12-month finding for a petition to list the Yellowstone cutthroat trout as threatened. Federal Register Volume 71:8818-8813.

Van Kirk, R.W. and L. Benjamin. 2001. Status and conservation of salmonids in relation to hydrologic integrity in the Greater Yellowstone Ecosystem. Western North American Naturalist 61:359-374.

Van Kirk, R.W. and M. Gamblin. 2000. History of fisheries management in the upper Henry's Fork watershed. Intermountain Journal of Sciences 6:263-284.

Van Kirk, R.W. and S.L. Hill. 2006. Modeling predicts trout population response to selenium based on individual-level toxicity. Final Report, Greater Yellowstone Coalition, Idaho Falls, ID.

Varley, J.D. 1979. Record of egg shipments from Yellowstone fishes, 1914-1955. U.S. National Park Service, Information Paper 36, Yellowstone National Park, WY.

Varley, J.D. and R.E. Gresswell. 1988. Ecology, status, and management of the Yellowstone cutthroat trout. Pages 13-24 *in* R.E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, MD.

Varley, J.D. and P. Schullery. 1983. Freshwater wilderness: Yellowstone fishes and their world. Yellowstone Library and Museum Association, Yellowstone National Park, WY.

Varley, J.D. and P. Schullery. 1995. The Yellowstone Lake crisis: confronting a lake trout invasion. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, WY.

Varley, J.D. and P. Schullery. 1998. Yellowstone fishes: ecology, history, and angling in the park. Stackpole Books. Mechanicsburg, PA.

Vashro, J. 1995. The "bucket brigade" is ruining our fisheries. Montana Outdoors 26:34-37.

Vincent, E.R. 1987. Effects of stocking catchable-size hatchery rainbow trout on two wild trout species in the Madison River and O'Dell Creek, Montana. North American Journal of Fisheries Management 7:91-105.

Visscher, L. 1984. Lewis Lake lake trout. U.S. Fish and Wildlife Service, Region 6, unpublished report, Denver, CO.

Wagner, E., R. Arndt, M. Brough, and D.W. Roberts. 2002. Comparison of susceptibility of five cutthroat trout strains to *Myxobolus cerebralis* infection. Journal of Aquatic Animal Health 14:84-91.

Walters, C. 1986. Adaptive management of renewable resources. Macmillan Publishing Company, New York, NY.

Walther, G.R., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J. Fromentin, O. Hoegh-Guldberg, and F. Gairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Wang, L. and R.J. White. 1994. Competition between wild brown trout and hatchery greenback cutthroat trout of largely wild parentage. North American Journal of Fisheries Management 14:475-487.

Ward, H.B. 1922. The Pelicans of Yellowstone Lake. Report to the U.S. National Park Service, Yellowstone National Park, WY.

Warren, C.E. and W.J. Liss. 1980. Adaptation to aquatic environments. Pages 15-40 *in* R.T. Lackey and L. Nielsen, editors. Fisheries management. Blackwell Scientific Publications, Oxford.

Welsh, J.P. 1952. A population study of Yellowstone blackspotted trout (*Salmo clarki*). Doctoral dissertation, Stanford University. Stanford, CA.

Westerling, A.L., H.G. Hidalgo, D.R. Cayan, and T.W. Swetnam. 2006. Warming and earlier spring increases western U.S. forest wildfire activity. Science 330:940-943.

Western Regional Climate Center. 2006. Website – http://www.wrcc.com. Desert Research Center. Reno, NV.

Williams, J.E., A.L. Haak, H.M. Neville, W.T. Colyer, and N.G. Gillespie. 2007a. Climate change and western trout: strategies for restoring resistance and resilience in native populations. Pages 236-246 *in* R.F. Carline and C. LoSapio, editors. Sustaining wild trout in a changing world; proceedings of Wild Trout IX symposium. Joseph Urbani and Associates, Bozeman, MT.

Williams, J.W., S.T. Jackson, and J.E. Kutzbach. 2007b. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences of the United States of America 104:5738-5742.

Winters, D.S. et al. 2004a. Aquatic, riparian and wetland ecosystem assessment for the Bighorn National Forest. Report 1 of 3. Introduction and ecological driver analysis. USDA Forest Service, Rocky Mountain Region, Denver, CO.

Winters, D.S. et al. 2004b. Aquatic, riparian and wetland ecosystem assessment for the Bighorn National Forest. Report 2 of 3: Anthropogenic influences report. USDA Forest Service, Rocky Mountain Region, Denver, CO.

Wishard, L., W. Christensen, and P. Aebersold. 1980. Biochemical genetic analysis of four cutthroat trout tributaries to the Idaho Blackfoot Reservoir system. Idaho Fish and Game, Final Report, Boise, ID.

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

Wolf, K., M.E. Markiw, and J.K. Hiltunen. 1986. Salmonid whirling disease: *Tubifex tubifex* (Muller) identified as the essential oligochaete in the protozoan life cycle. Journal of Fish Diseases 9:83-95.

Woodbury, L. A. 1934. Parasites and diseases of the trout of Yellowstone Lake: a biological account with special reference to the pathological aspects. Master's thesis. University of Utah, Salt Lake City, UT.

Woodward, D. F., A. M. Farag, M. E. Mueller, E. E. Little, and F. A. Vertucci. 1989. Sensitivity of endemic Snake River cutthroat trout to acidity and elevated aluminum. Transactions of the American Fisheries Society 118: 630-643.

Wyoming Game and Fish Department. 2005. Wyoming Game Fish Department management activities for Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*). Wyoming Game and Fish Department, Fish Division, Casper, WY.

The Yellowstone Cutthroat Trout Working Group. 1994. Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) management guide for the Yellowstone River drainage. Montana Department of Fish, Wildlife and Parks and Wyoming Game and Fish, Helena, MT and Cheyenne, WY.

Young, M.K. 1996. Summer movements and habitat use by Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in small, montane streams. Canadian Journal of Fisheries and Aquatic Sciences 53:1403-1408.

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.

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.

Zubik, R. 2007. Fisheries Biologist, USDA Forest Service, Region 2, Shoshone National Forest, Supervisor's Office, Cody, WY. Personal communication.

Zurstadt, C.F. and K. Stephan. 2005. Seasonal migration of westslope cutthroat in the Middle Fork Salmon River drainage, Idaho. Northwest Science 78:278-285.