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ARTICLE

Biology, Status, and Management of the Yellowstone Cutthroat Trout

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Abstract
Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* were historically distributed in the Yellowstone River drainage (Montana and Wyoming) and the Snake River drainage (Wyoming, Idaho, Utah, Nevada, and probably Washington). Individual populations evolved distinct life history characteristics in response to the diverse environments in which they were isolated after the last glaciation. Anthropogenic activities have resulted in a substantial decline (42% of the historical range is currently occupied; 28% is occupied by core [genetically unaltered] populations), but the number of extant populations, especially in headwater streams, has precluded listing of this taxon under the Endangered Species Act. Primary threats to persistence of Yellowstone cutthroat trout include (1) invasive species, resulting in hybridization, predation, disease, and interspecific competition; (2) habitat degradation from human activities such as agricultural practices, water diversions, grazing, dam construction, mineral extraction, grazing, timber harvest, and road construction; and (3) climate change, including an escalating risk of drought, wildfire, winter flooding, and rising temperatures. Extirpation of individual populations or assemblages has led to increasing isolation and fragmentation of remaining groups, which in turn raises susceptibility to the demographic influences of disturbance (both human and stochastic) and genetic factors. Primary conservation strategies include (1) preventing risks associated with invasive species by isolating populations of Yellowstone cutthroat trout and (2) connecting occupied habitats (where possible) to preserve metapopulation function and the expression of multiple life histories. Because persistence of isolated populations may be greater in the short term, current management is focused on isolating individual populations and restoring habitats; however, this approach implies that humans will act as dispersal agents if a population is extirpated because of stochastic events.

The Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* historically occurred in the Yellowstone River drainage in Montana and Wyoming and the Snake River drainage in Wyoming, Idaho, Utah, Nevada, and probably Washington (Behnke 1988; Figure 1). Individual populations of 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 (Gresswell et al. 1994). Although not as broadly distributed historically as either the westslope cutthroat trout *O. clarkii lewisi* or the coastal cutthroat trout *O. clarkii clarkii*, the Yellowstone cutthroat trout was probably more widely transplanted than any other subspecies of cutthroat trout *O. clarkii* (Varley and Gresswell 1988). Furthermore, because several million people from all over the world visit Yellowstone National Park each year, the Yellowstone cutthroat trout may be the fish that most people associate with the cutthroat trout (USFWS 2006; May et al. 2007).

Over the past century, anthropogenic activities have resulted in a substantial reduction in the historical distribution of the Yellowstone cutthroat trout, and many unique local populations have been extirpated (Meyer et al. 2003b; May et al. 2007). Numerous federal and state resource management agencies and nongovernmental 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 was submitted in 1998 (Biodiversity Legal Foundation et al. 1998). Although listing was found to be unwarranted in 2001 (USFWS 2001), a court-ordered

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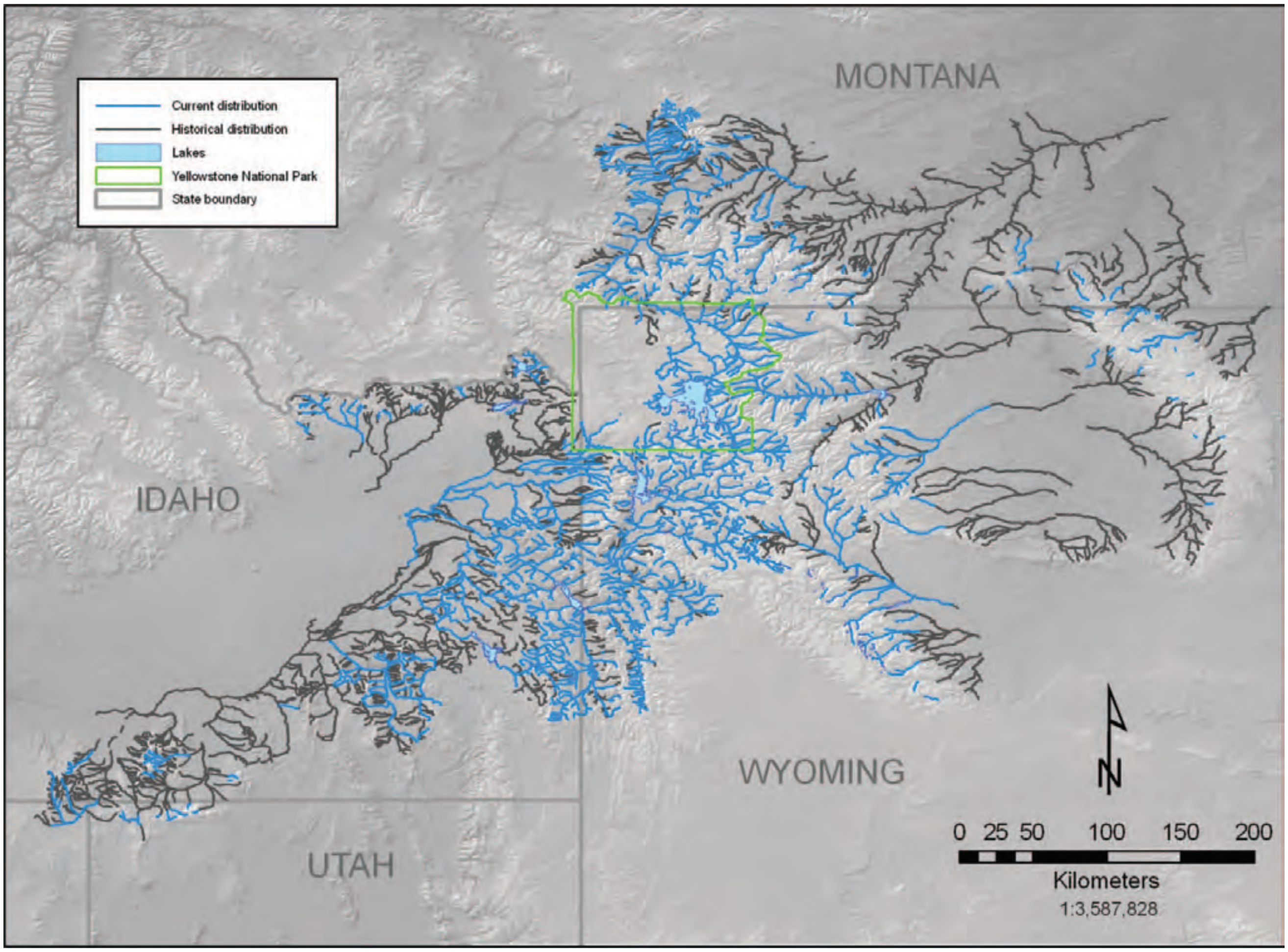

FIGURE 1. Current distribution (blue) of Yellowstone cutthroat trout superimposed on the putative historical (black) distribution of the subspecies (May et al. 2007; MDFWP 2008).

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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% of the historical range is currently occupied; 28% is occupied by core [genetically unaltered] populations; Tables 1, 2; Figure 2), the presence of many populations, especially in headwater streams, has precluded listing of this subspecies under the Endangered Species Act (USFWS 2006). 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 illegal introduction of nonnative lake trout *Salvelinus namaycush* into Yellowstone Lake, the spread of *Myxobolus cerebralis* (the causative agent of whirling disease), and drought in the Intermountain West have resulted in population declines in many areas.

An initial review of the status and management of the subspecies was published in the late 1980s (Varley and Gresswell 1988), and a subsequent update was published in 1995 (Gresswell 1995). During the past 15 years, however, a substantial amount of new information on the distribution, biology, management, and legal status of Yellowstone cutthroat trout has emerged, but there has not been an updated synthesis.

TABLE 1. Currently occupied stream habitat (km; and expressed as a percentage of historically occupied habitat) in each state within the historical range of Yellowstone cutthroat trout (source: May et al. 2007).

State	Currently occupied stream habitat (km)	Current habitat as a percentage of historically occupied habitat
Wyoming	6,515	60
Idaho	3,272	30
Montana	2,155	31
Nevada	93	38
Utah	79	52
Total	12,114	42

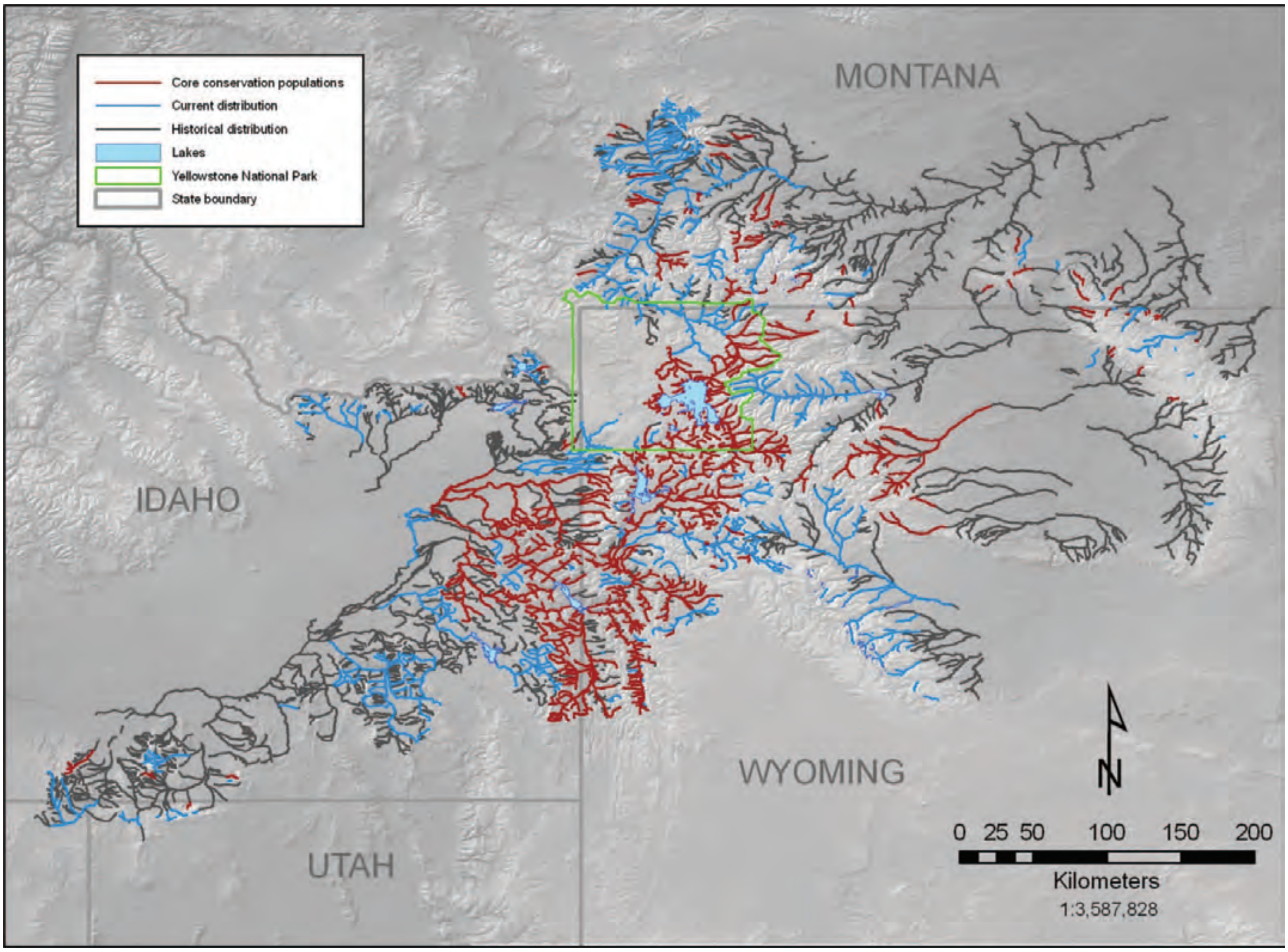

FIGURE 2. Core conservation (red) population distributions of Yellowstone cutthroat trout superimposed on the current (blue) and putative historical (black) distributions of the subspecies (May et al. 2007; MDFWP 2008).

To that end, the present assessment examines the biology, ecology, conservation status, and management of the Yellowstone cutthroat trout and provides a synthetic review of the reproductive behavior, population dynamics, and life history characteristics of this subspecies. Although the synthesis focuses on current environmental conditions, future management options are also considered. The Snake River finespotted cutthroat trout *O. clarkii behnkei* cannot currently be distinguished genetically from the Yellowstone cutthroat trout, and the ranges of these two taxa overlap (Behnke 2002); thus, for the purposes of this review, the Snake River finespotted cutthroat trout is considered a morphologically divergent ecotype of the more broadly distributed Yellowstone cutthroat trout.

TABLE 2. Origin of lacustrine assemblages of Yellowstone cutthroat trout by state, number of lakes, and surface area (source: MDFWP 2010).

	Native populations		Introduced populations		Unknown origin	
State	Lakes	Area (ha)	Lakes	Area (ha)	Lakes	Area (ha)
Wyoming	54	38,198	131	1,774	2	30
Idaho	6	18,636	3	5	0	
Montana	0		26	240	2	42
Total	60	56,834	160	2,019	4	72

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 (May et al. 2007). Because the U.S. 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 (USFWS) 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 (May et al. 2007).

Yellowstone cutthroat trout populations, regardless of their genetic status, are managed as sport fish in the states and national parks. Beyond this basic management strategy, a hierarchical classification for conserving the genetic integrity of cutthroat trout has been adopted (UDWR 2000). 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 that have attributes worthy of conservation, and (3) populations that are managed primarily for their recreational fishery value (May et al. 2003). Core conservation populations have important genetic value and can be used to develop captive broodstocks 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, two basic and somewhat conflicting management strategies are being used to conserve Yellowstone cutthroat trout. One strategy focuses on preventing risks associated with nonnative species (e.g., introgression, disease, predation, and competition) by isolating populations of Yellowstone cutthroat trout (May et al. 2003). Although the persistence of isolated populations may be greater in the short term, this strategy implies that humans will act as dispersal agents if a population becomes extirpated because of stochastic events. The second strategy concentrates on connecting occupied habitats to preserve metapopulation function and multiple life history strategies. In addition, numerous projects are addressing habitat restoration or nonnative species removal at a local scale (May et al. 2007).

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 (U.S. Forest Service and National Park Service) in the area (MDFWP et al. 2000). An updated conservation agreement was promulgated in 2010 (RYCTCT 2009a). The goal of the conservation effort is "to ensure the persistence of Yellowstone cutthroat trout within the historical range." Current objectives include (1) identification of existing populations, (2) protection and enhancement of conservation populations, (3) restoration of extirpated populations, (4) protection and enhancement of watershed conditions, (5) public outreach, (6) data sharing, and (7) coordination among agencies (RYCTCT 2009a). In Montana, Wyoming, and Idaho, conservation plans have been developed specifically for Yellowstone cutthroat trout; in Utah and Nevada, conservation of the subspecies is addressed as part of more general 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. A conservation strategy has been developed to implement coordinated management of the Yellowstone cutthroat trout, and it provides a framework for the interagency group (RYCTCT 2009b). Specific management actions are outlined in the strategy, and it is evaluated annually and modified as necessary to maintain relevancy and effectiveness and to ensure that the program is effective (RYCTCT 2009b).

BIOLOGY AND ECOLOGY

Systematics and General Species Description

The Yellowstone cutthroat trout is one of 14 subspecies of cutthroat trout suggested by Behnke (1988) and is classified among the four major cutthroat trout subspecies (Behnke 1988, 1992). Systematists do not agree on the evolutionary history of cutthroat trout (Behnke 1992; Stearley 1992; Smith et al. 2002), but fossil evidence suggests that many species of western trout (including cutthroat trout) originated in the Great Basin during the Miocene (Stearley and Smith 1993; Smith et al. 2002). According to Behnke (1992), rainbow trout *O. mykiss* replaced Yellowstone cutthroat trout in the Columbia River basin below Shoshone Falls (Idaho) on the Snake River sometime after a late-glacial flood event formed the falls (14,500 years before present; 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 cutthroat trout into the Yellowstone River drainage was associated with the retreat of glacial ice that occurred about 12,000 years before present (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 a variety of genetic techniques (Campbell et al. 2002). For example, allozyme analysis has provided at least 10 loci that are diagnostic between the two species (Leary et al. 1987, 1989; Allendorf and Leary 1988). Nuclear and mitochondrial DNA (mtDNA) can be extracted from small amounts of tissue, and both types of DNA can be used to differentiate cutthroat trout 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 cutthroat trout, Yellowstone cutthroat trout, and Rio Grande cutthroat trout *O. clarkii virginalis*; Leary et al. 1995).

Metapopulations of Yellowstone cutthroat trout evolved unique life history characteristics in response to the 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). There was only one other native fish in Yellowstone Lake, but the metapopulation in Heart Lake (Snake River drainage, Yellowstone National Park) 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 nonnative 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 the subspecies was subsequently replaced by rainbow trout below Shoshone Falls and by rainbow trout and westslope cutthroat trout in the Salmon and Clearwater River drainages. To investigate more recent changes, May et al. (2003) suggested that 1800 (the approximate year of European settlement of the interior portions of the western United States) was a reasonable reference point 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 about 44,500 ha of lake area. Analysis based on an updated hydrography and advanced mapping tools yielded more precise estimates of historical fluvial habitat (~28,519 km; Table 1) and lake habitat (60 lakes, ~56,834 ha; Table 2; May et al. 2007).

Introduction of nonnative fishes (resulting in hybridization, predation, disease, and interspecific competition), habitat degradation (from human activities such as 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. Population declines and extirpations of Yellowstone cutthroat trout have been greatest in larger, low-elevation streams where human activities (e.g., agriculture, livestock grazing, and resource extraction) are common and where unrestricted access facilitates angler harvest and nonnative species introductions (Gresswell 1995; Thurow et al. 1997). The remote location of some 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) have provided 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% of the stream kilometers currently occupied by Yellowstone cutthroat trout occur on federal or tribal government lands and 28% are being managed as part of national parks or federally designated wilderness (May et al. 2007). Although location in these areas undoubtedly reduces the probability of anthropogenic perturbations, negative consequences of the illegal introduction of lake trout into 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 the persistence of genetically unaltered populations of Yellowstone cutthroat trout.

According to the most recent status assessment, Yellowstone cutthroat trout are most broadly distributed in three states: 54% of currently occupied stream habitat is located in Wyoming, 27% is located in Idaho, and 18% is located in Montana (Table 1). Although the currently occupied stream habitat in Nevada and Utah collectively represents only about 1.5% of the total, the proportion of historically occupied habitat in each of these states is actually greater than that in either Idaho or Montana (Table 1; May et al. 2007). Occupancy is lowest in habitats near the fringe of the historical range, especially the Snake River (downstream of the Portneuf River), middle Yellowstone River, and lower Bighorn River systems (May et al. 2007). The fact that most populations occupy less than 16 km of stream (May et al. 2007) suggests substantial habitat fragmentation, and this is a major source of concern for the persistence of the subspecies.

Varley and Gresswell (1988) estimated that genetically unaltered populations of Yellowstone cutthroat trout occurred in approximately 10% of the historical stream habitat and about 85% of the historical lake habitat; however, these estimates were based largely on the potential for introgression by transplanted rainbow trout or other cutthroat trout subspecies. Studies with a stronger empirical basis provide more optimistic estimates. Based on genetic samples (6,249 km) and professional opinion (no record of stocking or presence of contaminating species; 2,984 km), May et al. (2007) suggested that up to 28% (assuming no introgression in areas for which data are based on professional opinion) of the historical range of Yellowstone cutthroat trout still supported populations that were genetically unaltered conservation populations (Table 3). Introgression varies across the historical range of the Yellowstone cutthroat trout, however, and it appears that 14–65% of the stream habitat in specific geographical areas still supports genetically unaltered populations (May et al. 2007). Furthermore, 163 (80%) of the 205 lakes that are currently occupied by Yellowstone cutthroat trout support genetically unaltered populations (May et al. 2007). When

TABLE 3. Genetic status of Yellowstone cutthroat trout in terms of occupied stream length (km) within the subspecies' current range (source: May et al. 2007).

Genetic status	Occupied stream length (km)	Percentage of total currently occupied habitat
Tested; unaltered ($<$1% introgression)	5,008	41
Tested; $\geq$1% to $\leq$10% introgression	985	8
Tested; $>$10% to $\leq$25% introgression	166	1
Tested; $>$25% introgression	90	1
Suspected to be unaltered	2,984	25
Potentially altered	2,597	21
Mixed stock (altered and unaltered)	272	2
Not applicable	11	0
Total	12,114	100

persistence criteria related to effective habitat size were applied to core conservation populations in streams, 36% of the populations met persistence criteria and 64% did not (Haak et al. 2010).

Population Trend

Several studies provide updated information concerning population trends of Yellowstone cutthroat trout in the historical range. The Yellowstone Cutthroat Trout Interagency Coordination Group summarized many of these studies in the 2006 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 was included in the update (May et al. 2007).

Numerous studies document more specific trend information. For example, for almost 20 years after the original samples of 77 stream sites from southeastern Idaho, relative abundance and size structure remained quite consistent (Meyer et al. 2003b). During this period, the number of sites with introgressed populations rose from 23 to 37 (30–48% of the total number of sites), but it appeared that most of the changes occurred at 17 sites located in the Blackfoot River and South Fork Snake River drainages (Meyer et al. 2003b).

In Montana, introgression with nonnative 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 ($\approx$0.2%; Shepard and Snyder 2005). In contrast, many fluvial populations have been reclassified from genetically unaltered ($<$1% introgression detected) or hybridized (1–25% introgression) populations to mixed-stock populations ($>$25% introgression). Some of these changes reflect data corrections rather than an expansion of introgressed populations.

Population trends in Wyoming were updated for the rangewide status review of the Yellowstone cutthroat trout (May et al. 2007). Conversion to a 1:24,000-scale hydrographic coverage revealed about 320 km of currently occupied streams in Wyoming that were not previously displayed on the 1:100,000-scale hydrographic coverage used for the 2001 assessment (WGFD 2005; May et al. 2007). Furthermore, based on stream survey data collected since 2001 (WGFD 2005), it appears that genetically unaltered Yellowstone cutthroat trout occupy an additional 491 km of historical habitat within the state.

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. Although National Park Service policies provide substantial habitat protection from the pollution and land use practices that often degrade salmonid habitats, native trout were subjected to the effects of nonnative 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-1980s, however, it appeared that the assemblage of Yellowstone cutthroat trout in Yellowstone Lake was relatively secure (Gresswell et al. 1994).

Since the early 1990s, the introduction of nonnative lake trout, invasion by the parasite *M. cerebralis* (the causative agent of whirling disease), and many years of below-average precipitation in the Yellowstone Lake drainage (6 of the 10 years from 1996 to 2005; WRCC 2006) have resulted in serious new declines in Yellowstone cutthroat trout abundance (Koel et al. 2005). Angler landing rates for Yellowstone cutthroat trout declined from 2.0 fish/h in 1994 to 0.8 fish/h in 2004 (Koel et al. 2005). Monitoring programs that target fish ascending tributaries to spawn and annual fall gillnetting assessments provide further evidence of 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 in 1977–1992 (Gresswell et al. 1994) to 3,828 in 2001–2004 (Koel et al. 2005). The number of spawners in 2006 (471) was the lowest recorded in the 60-year period of record (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 in Pelican Creek is no longer operational; however, recent sampling with nets at the historical weir site suggests that Yellowstone cutthroat trout from the lake no longer enter the tributary (Koel et al. 2005). Similar declines in the abundance of spawners have been noted for 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. On average, 15.9 Yellowstone cutthroat trout/net were caught in 1994, but by 2002 the estimate had declined to only 6.1 Yellowstone cutthroat trout/net (Koel et al. 2005). Reductions averaged 11% per year between 1994 (the year in which 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 section).

In addition to undertaking reproductive migrations, salmonids may seasonally move to feeding or refuge habitats (Northcote 1997). For instance, movement to winter refugia has been well documented for some salmonids (Cunjak and Power 1986). 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 these movements in Yellowstone cutthroat trout. In the Snake River near Jackson, Wyoming (mean annual discharge = 107 m^3/s), Harper and Farag (2004) reported movements to winter refugia by Snake River finespotted cutthroat trout during the winter. As water temperature declined below 1.0°C, radio-tagged 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). However, recent research suggests that movement (migratory and nonmigratory) of cutthroat trout is common in headwater streams (Young et al. 1997; Peterson and Fausch 2003; 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).

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; Varley and Gresswell 1988). Fluvial populations were historically common in large rivers, such as the Snake River above Shoshone Falls (mean annual discharge = 156 m^3/s) and the Yellowstone River near Livingston, Montana (mean annual discharge = 107 m^3/s; 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; Isaak and Hubert 2000). Using data collected at 151 sites in 56 perennial watersheds within the Greybull River–Wood River drainage (northwestern Wyoming), Kruse et al. (1997) correctly classified the presence or absence of Yellowstone cutthroat trout at 83% of the sites by use of gradient alone. Adding stream length and elevation to the predictive model increased the rate of correct classification to 87%. No wild Yellowstone cutthroat trout populations were found above barriers to migration (Kruse et al. 1997). In the Salt River basin (Idaho and Wyoming), cutthroat trout densities were greatest in high-gradient reaches with a diversity of pools, riffles, and runs where densities of brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* were low (Quist and Hubert 2005).

Yellowstone cutthroat trout are often found in cold, harsh environments. Water temperatures between 4.5°C and 15.5°C are common for areas occupied by this subspecies (Carlander 1969). During experiments conducted by Dwyer and Kramer (1975) on cultured cutthroat trout (age 1 and older), the maximum scope for activity (the difference between maximum and minimum metabolic rates) occurred at 15°C. Mean daily water temperature for July and August in 11 watersheds of southeastern Idaho ranged from 6.8°C to 12.9°C (Meyer et al. 2003a). Isaak and Hubert (2004) reported that the relationship between Yellowstone cutthroat trout populations (density and biomass) and mean summer (July and August) stream temperature at 57 sites in the Salt River watershed (Wyoming) was best represented by dome-shaped curves. Peaks in curves for allopatric Yellowstone cutthroat trout populations occurred near 12°C; predicted *x*-intercepts were near 3°C and 21°C. In Yellowstone National Park, some populations of Yellowstone cutthroat trout exist in streams with summer maxima between 5°C 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 that were collected beneath 1 m of ice in Yellowstone Lake appeared to be actively feeding in 0–4°C water (Jones et al. 1979).

In large rivers, habitat complexity may be critical for overwinter survival. For instance, Snake River finespotted 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 below 1.0°C, adults and juveniles move to off-channel pools with groundwater influence. Although these habitats are used frequently under low-temperature conditions, they are not common in the study area examined by Harper and Farag (2004). Those authors suggested that the multidimensional characteristics of the off-channel pools with groundwater influence (e.g., water depth, temperature, cover, and habitat stability) were important during cold periods.

In the South Fork Snake River (mean annual discharge 1950–1990 = 189 m^3/s; USGS 1991), Yellowstone cutthroat trout are sympatric with brown trout, and age-0 individuals of both species remain concealed at water depths less than 0.5 m during February–April (Griffith and Smith 1993). Griffith and Smith (1993) reported that Yellowstone cutthroat trout were abundant in boulder substrates but could not be found in rounded cobble; few brown trout or Yellowstone cutthroat trout were found in areas 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 Snake River finespotted 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 based on availability, but both taxa 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, warmwater populations have yet been documented; however, several populations occur in geothermally heated streams in Yellowstone National Park. In these streams, which have an ambient water temperature of 27°C, Yellowstone cutthroat trout apparently survive by finding thermal refugia (Varley and Gresswell 1988); however, Schrank et al. (2003) suggested that heat shock proteins may contribute to the survival of Bonneville cutthroat trout *O. clarkii utah* during brief periods of excessively high water temperature. In contrast, Kelly (1993) suggested that summer water temperatures exceeding 22°C excluded Yellowstone 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, in Yellowstone National Park, this subspecies has been collected from waters with total dissolved solids ranging from about 10 to 700 mg/L (Varley and Gresswell 1988). Meyer et al. (2003a) 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 upper Snake River basin waters with alkalinity levels exceeding 150 mg $CaCO_3$/L (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 (from 5.6 to over 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 that widely fluctuating pH resulting from poor buffering capacity precluded the 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 Snake River tributaries between Jackson Lake and Palisades Reservoir; total dissolved solids at these sites ranged from 134 to 258 mg/L.

Less has been documented concerning the habitat of lacustrine populations of Yellowstone cutthroat trout. Prior to the discovery of lake trout in Yellowstone Lake (1994), most juvenile Yellowstone cutthroat trout (age $<$ 3) occupied pelagic areas (Gresswell and Varley 1988) and mature individuals were found in the littoral zone of the lake (Gresswell and Varley 1988). The vast size of the pelagic area appeared to provide protection from predation by avian piscivores and larger Yellowstone cutthroat trout. Gresswell and Varley (1988) assumed that 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. However, this relationship with pelagic habitat evolved in a system where piscivorous fish were uncommon, and the effects of introduced lake trout on current distribution patterns of juvenile Yellowstone cutthroat trout 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 of Yellowstone cutthroat trout are uncommon, trout in streams generally feed on drift, benthic invertebrates, and other fish. Research with coastal cutthroat trout suggests a strong terrestrial influence on drift in some headwater streams where there is a strong 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) reported that Yellowstone cutthroat trout are generally more piscivorous than westslope cutthroat trout, but evidence of fish consumption by Yellowstone cutthroat trout is uncommon. One definite anomaly occurs in Heart Lake, where piscivorous 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 and fed on zooplankton, larger crustaceans, and aquatic insects (Benson 1961; Jones et al. 1990). Tronstad et al. (2010) documented a direct relationship between inter-gill raker spaces and body length, but it appeared that Yellowstone cutthroat trout could feed on zooplankton throughout their lives. Although native longnose dace *Rhinichthys cataractae* and introduced populations of redside shiners *Richardsonius balteatus*, lake chub *Couesius plumbeus*, and longnose suckers *Catostomus catostomus* also occupy the littoral areas of Yellowstone Lake, piscivory by Yellowstone cutthroat trout was historically uncommon (Benson 1961; Jones et al. 1990).

BREEDING BIOLOGY

Four migratory spawning patterns have been described for Yellowstone cutthroat trout (Varley and Gresswell 1988). 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 may remain near the redd (Varley and Gresswell 1988). In larger rivers, it appears that fluvial spawners may co-occur with individuals that exhibit a fluvial–adfluvial migration pattern (Henderson et al. 2000; DeRito et al. 2010). Furthermore, Yellowstone cutthroat trout spawning in the Yellowstone River between Yellowstone Lake and the Upper Falls (28 km) appear to be a mixture of fluvial spawners from the river and allacustrine spawners (described below) from Yellowstone Lake (Ball and Cope 1961; Kelly 1993; Kaeding and Boltz 2001).

Fluvial–adfluvial populations migrate from streams into tributaries to spawn. This pattern has been documented in the Yellowstone River (Montana; Clancy 1988; Byorth 1990; DeRito et al. 2010), several Snake River drainages (Idaho; Thurow et al. 1988; Henderson et al. 2000), and the Yellowstone River (below the Lower Falls) and Lamar River (Yellowstone National Park; Varley and Gresswell 1988). Juveniles may emigrate as fry or spend 1–3 years in natal tributaries before returning to the main stem (Thurow et al. 1988; Varley and Gresswell 1988).

Lacustrine–adfluvial populations live in lakes and ascend tributaries to spawn (e.g., Gresswell et al. 1994, 1997). 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 (>2 years) lotic residency for some Yellowstone cutthroat trout that were spawned in Pelican Creek, a tributary of Yellowstone Lake (Gresswell et al. 1994).

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 (USFWS, 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).

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 habitat patches are believed to provide growth and refuge advantages compared with smaller tributary systems; however, in some large tributaries and the Yellowstone River below the lake, postspawn residency extends 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). Because iteroparity is related to gonad development, it can be affected by parasitic infection and other physiological factors that influence growth (Ball and Cope 1961). There is also evidence that angler harvest can affect the proportion of repeat spawners. For example, during the 1950s, when angler harvest was high (200,000–400,000 Yellowstone cutthroat trout annually; Gresswell and Varley 1988), Ball and Cope (1961) estimated that first-time spawners comprised up to 99% of the spawning migrations in Yellowstone Lake. After angler harvest reductions occurred in the early 1970s, more than 20% of the Yellowstone cutthroat trout that were marked at Clear Creek in 1979 returned to spawn again between 1980 and 1984 (Jones et al. 1985). Up to 15% of Yellowstone cutthroat trout in some fluvial and fluvial–adfluvial migrations in Idaho had spawned previously (Thurow et al. 1988), and most (93%) of the repeat spawners were females (Thurow 1982).

Repeat spawners may return in consecutive or alternate years (Thurow et al. 1988; Varley and Gresswell 1988). Alternate-year spawning appears to be more common in iteroparous populations at higher elevations (Varley and Gresswell 1988), but Bulkley (1961) concluded that consecutive-year spawners were more common in tributaries to Yellowstone Lake (elevation = 2,357 m). After 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 1980s, consecutive-year spawners in the Yellowstone River between Corwin Springs and Springdale (Montana) consistently exhibited the slowest growth (Clancy 1988).

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); with regard to 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 spawners in the Yellowstone River (Montana; Clancy 1988; DeRito et al. 2010), tributaries to Yellowstone Lake (Cope 1957a; Gresswell et al. 1994; Gresswell et al. 1997), and the Blackfoot and South Fork Snake rivers in Idaho (Thurow et al. 1988; Henderson et al. 2000). Straying during the spawning migration is low—generally 1–3% for iteroparous spawners monitored in large lakes and rivers (Cope 1957a; Thurow 1982; Jones et al. 1985). Similar estimates have been reported for fluvial and allacustrine spawners (Kaeding and Boltz 2001; DeRito et al. 2010); however, sample sizes were small. 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).

Spawning streams are most commonly perennial and have groundwater and snow-fed water sources. The stream gradient at spawning areas is usually less than 3% (Varley and Gresswell 1988), but nonmigratory fluvial populations have been documented in streams with a mean gradient of 6% (Meyer et al. 2003a). Yellowstone cutthroat trout were not present at any of 151 locations in northwestern Wyoming when gradient was 10% or higher or when elevation was greater than 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 the fry emigrate in July and August before late-summer desiccation. Although many fry and some adults may become stranded as discharge declines, spawning in intermittent streams may provide a reproductive advantage over nonnative 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; DeRito et al. 2010). The timing of migration into a specific watershed reflects physical characteristics (e.g., latitude, elevation, and aspect) that influence annual discharge patterns and stream temperature (Gresswell et al. 1997; Henderson et al. 2000; Meyer et al. 2003a); therefore, spawning may occur earlier at lower elevation sites. The average size of spawners, however, appears to reflect conditions that influence growth and survival in areas occupied during nonreproductive periods (Gresswell et al. 1997).

Spawning has been documented at water temperatures between 5.5°C and 20°C (Varley and Gresswell 1988; Byorth 1990; Meyer et al. 2003a), but water temperatures in spawning areas are generally above 10°C. During migration, spawner abundance generally increases as water temperature rises and discharge decreases from the spring runoff peak (Varley and Gresswell 1988; Byorth 1990; Thurow and King 1994). 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. 1997).

Nocturnal migration of salmonid spawners is uncommon (Carlander 1969); however, Yellowstone cutthroat trout spawners have been observed to migrate throughout the day and night. In most cases, upstream migration appears to occur diurnally, but patterns may vary locally depending water temperature (Thurow 1982; Varley and Gresswell 1988; USFWS, unpublished data; National Park Service, unpublished data). Upstream movement generally reaches a daily maximum in concordance with increasing water temperature and decreasing discharge (Byorth 1990; Jones et al. 1990). However, there is some evidence that anthropogenic activities, such as angler harvest and spawn-taking operations, may also affect daily movement patterns (Gresswell 1995). Emigration of Yellowstone cutthroat trout postspawners is often nocturnal prior to peak discharge, whereas during the later portion of the annual migration, downstream movement usually occurs during the day (Varley and Gresswell 1988).

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 these early migrants usually move farther upstream than later migrants (Cope 1957b; Dean et al. 1975). Age, length, weight, and condition factor decline as the spawning migration progresses (Jones et al. 1990). Gender also influences migration timing, as males usually migrate into spawning tributaries earlier than females (Ball and Cope 1961). Similar behavior has been noted for other migratory fishes (Briggs 1955).

Yellowstone cutthroat trout spawners remain in tributaries to Yellowstone Lake for 6–25 d (Varley and Gresswell 1988). Time spent in spawning areas is usually greater for males than for females. In some larger tributaries, lacustrine–adfluvial spawners maintain a tributary residence for many months (Gresswell et al. 1994), and a similar pattern has been reported for allacustrine spawners downstream from a lake (Schill and Griffith 1984; Kaeding and Boltz 2001). During the initial portion of adfluvial spawning migrations, some individuals move into and out of tributaries repeatedly before spawning (USFWS, unpublished data).

Optimum gravel size in Yellowstone cutthroat trout spawning areas is 12–85 mm in diameter (Varley and Gresswell 1988), but spawning has been documented in areas with substrate diameters less than 6.4 mm and greater than 100 mm (Byorth 1990; Thurow and King 1994). Where discharge volume and movement of fine sediments limit spawning in main-stem rivers and where the potential for recruitment is low in tributaries, spring creeks may be critical areas for spawning (Hayden 1967; Kiefling 1978).

Varley and Gresswell (1988) suggested that Yellowstone cutthroat trout spawn wherever they find optimum temperature and substrate; however, other factors determine use in specific localities. For example, research in tributaries to Yellowstone Lake suggested that spawners were not always associated with areas having the greatest concentration of spawning gravel and that forest cover did not affect the distribution of redds (Cope 1957b). Furthermore, 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, and these characteristics vary annually in conjunction with stream discharge (Thurow and King 1994).

Information concerning Yellowstone cutthroat trout spawning sites is sparse. Thurow and King (1994) reported that mean redd size ($n = 66$) was 1.58 m long $\times$ 0.60 m wide and that redds covered an area of approximately 1 m^2. Water depth at spawning areas is usually less than 60 mm, but most redds are found in water depths of 10–30 cm (Thurow and King 1994). In smaller tributaries, redds occur at the lower end of the depth range (Byorth 1990). Water velocity next to the redds of Yellowstone cutthroat trout falls in the range of 16–73 cm/s (Byorth 1990; Thurow and King 1994). Mean velocity is generally greater in larger streams (42 cm/s beside the redd and 46 cm/s upstream from the redd; Thurow and King 1994) than in smaller tributaries (24–38 cm/s; Byorth 1990).

Superimposition of redds is common in Yellowstone cutthroat trout spawning streams (Mills 1966; Byorth 1990). It is apparent, however, that superimposition generally occurs laterally or immediately downstream of existing redds (Thurow and King 1994). Therefore, it may not disturb developing embryos because the eggs are often deposited in the center of the tailspill's upstream edge (Thurow and King 1994).

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

DEMOGRAPHY

Although robust populations of Yellowstone cutthroat trout are broadly distributed 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 nonnative trout, and it is believed that many of these populations are 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 nonnative 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 the 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. 2008b).

Genetic Characteristics and Concerns

To thoroughly comprehend and protect the diversity and complexity of the Yellowstone cutthroat trout, it is important to gain a better understanding of the factors influencing the observed variation in phenotypic traits. Although it might be reasonable to assume that there is a strong genetic component to that variation, evidence in support of that assumption is lacking and there are few genetic data that can be used to characterize groups of Yellowstone cutthroat trout. In fact, initial examination of genetic structure of the subspecies by use of allozyme data suggested that the Yellowstone cutthroat trout underwent a geologically recent genetic bottleneck during the Pleistocene glaciation. Loudenslager and Gall (1980) found that only 8% of the genetic diversity among 10 Yellowstone cutthroat trout populations distributed over a broad geographical range 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 the genetic structure of Yellowstone cutthroat trout in Yellowstone Lake based on protein electrophoresis and mtDNA failed to detect genetic differences among spawning populations (Shiozawa and Williams 1992).

With the advent of genetic techniques that provide the ability to differentiate fine-scale variation and reproductive isolation among species, it is now possible to gain new insights into the structure of Yellowstone cutthroat trout distribution. For example, 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 (among the 11 major river drainages 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 were more altered by anthropogenic activities (Cegelski et al. 2006).

Another recent study that examined microsatellite loci failed to find significant genetic differentiation among spawning populations from Yellowstone Lake by use of 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 and over 50 years of potential genetic mixing caused by the hatchery operation on Yellowstone Lake (Gresswell and Varley 1988). These results may provide some insight into observed phenotypic variation among spawning populations in tributaries to the lake (Gresswell et al. 1994, 1997).

The taxonomic status of the Snake River finespotted cutthroat trout (Behnke 1992) is complex and controversial. The large-spotted form of the Yellowstone cutthroat trout was historically found throughout the range of the subspecies (Varley and Gresswell 1988; Behnke 1992). In contrast, the fine-spotted 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 large-spotted form is common in the Snake River headwaters and in many 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 that used mtDNA and six microsatellite loci failed to find genetic differences between the 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 (Wyoming). The second common clade was found more frequently in the Hoback River, Snake River Canyon, and Greys River (Novak et al. 2005).

Efforts to identify genetically unaltered populations of Yellowstone cutthroat trout are an integral part of current management of the subspecies throughout its range, and the importance of this effort has been formalized by the Rangewide Yellowstone Cutthroat Trout Conservation Team (RYCTCT 2009a). In the Yellowstone River drainage, both in Yellowstone National Park and in Montana, genetic sampling has been pursued vigorously in recent years. Strategies that have been officially recognized by the interagency conservation team (May et al. 2007; RYCTCT 2010b) include the protection of Yellowstone cutthroat trout populations with genetic purity of 99% or higher and the genetic restoration of introgressed populations.

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

The use of piscicides to remove undesirable fishes has a long history in the United States, but employing this technique to protect indigenous species from hybridization and competition with other salmonid species was infrequent until the 1980s (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). There have been some attempts to remove nonnative salmonids by use of electrofishing in order to avoid the negative consequences associated with pesticides (Thompson and Rahel 1998; Kulp and Moore 2000; Peterson et al. 2008a); however, success has been mixed (Finlayson et al. 2005; Meyer et al. 2006a). Although renovation may be critical for the protection and reintroduction of Yellowstone cutthroat trout in some areas, it is extremely expensive and long-term success is difficult to achieve (Finlayson et al. 2005).

Age and Growth

Yellowstone cutthroat trout in Idaho live to 8 or 9 years of age; maximum lengths are greater than 600 mm, and maximum weights range from 2 to 4 kg (all lengths presented throughout are total length; Thurow et al. 1988). In Heart Lake, where Yellowstone cutthroat trout are believed to be highly piscivorous, maximum weight can exceed 5 kg. Prior to the discovery of lake trout in Yellowstone Lake, Yellowstone cutthroat trout larger than 500 mm and 1.5 kg were uncommon. However, in 2008, the mean length of spawners entering Clear Creek was 532 mm, and the maximum size of Yellowstone cutthroat trout captured in annual monitoring with gill nets exceeded 600 mm (Koel et al. 2010).

In Henrys and Yellowstone lakes, males historically grew faster than did females (Irving 1955; Bulkley 1961), and the largest individuals in Yellowstone Lake were males. Although Varley and Gresswell (1988) speculated that the latter observation was due to greater longevity rather than to faster growth, it is possible that physiological demands are greater for maturing ova than for male gamete development. In fact, prior to the introduction of lake trout, many of the largest individuals (>450 mm) in Yellowstone Lake were immature (Gresswell 1995). When the annual growing season is short, somatic growth may be encouraged by postponing maturity and the associated demands of gonadal development.

Age analysis for Yellowstone cutthroat trout has primarily been based on fish scales, but validation of the technique has only been completed to age 2 (Laakso and Cope 1956). In Yellowstone Lake, scales are formed when larvae are approximately 41–44 mm (Brown and Bailey 1952; Laakso and Cope 1956). Laakso and Cope (1956) reported that some individuals in Yellowstone Lake do not form an annulus until the end of the second year of growth, and they established criteria to distinguish "normal" and "retarded" (annulus not formed at the end of the first year) scale formation. Although Laakso (1955) argued that the criteria are generally applicable, information from other cutthroat trout subspecies suggest that these criteria are not universal (Heck 2007). Lentsch and Griffith (1987) reported that across the range of the Yellowstone cutthroat trout, development of a first-year annulus was related to temperature in the natal stream. When the number of accumulated temperature units (sum of mean daily temperatures above 0°C) during the growing season was 720 or fewer, all individuals lacked an annulus at the end of the first season of growth (Lentsch and Griffith 1987). If the number of accumulated temperature units was 1,500 or higher, all fish formed an annulus at the end of the first year (Lentsch and Griffith 1987).

There has been a plethora of aging studies for Yellowstone cutthroat trout based on scale analyses (e.g., Irving 1955; Laakso 1956; Laakso and Cope 1956; Bulkley 1961; Benson and Bulkley 1963; Thurow 1982; Moore and Schill 1984; Shepard 1992). Back-calculated lengths for Yellowstone cutthroat trout (Carlander 1969) have been summarized as 100 mm at age 1; 180 mm at age 2; 240 mm at age 3; 310 mm at age 4; 370 mm at age 5; and 410 mm at age 6 (Varley and Gresswell 1988). Growth of Yellowstone cutthroat trout from Yellowstone Lake for 20 years between 1969 and 1992 was estimated to be 60 mm at age 1; 140 mm at age 2; 240 mm at age 3; 310 mm at age 4; 350 mm at age 5; 390 mm at age 6; 420 mm at age 7; 450 mm at age 8; and 470 mm at age 9 (USFWS, unpublished data).

Despite broad acceptance of the technique, Hubert et al. (1987) found that the precision of age determinations from scales was not high and that there was a bias related to the lack of a first-year annulus on many scales. Although the precision of estimates based on otoliths was not significantly different, otoliths could be used to reduce age bias with scales. Combining the two techniques was encouraged in order to increase the accuracy of age analyses (Hubert et al. 1987).

Younger and smaller Yellowstone cutthroat trout grow faster than older and larger individuals do, but growth varies with environmental conditions. Gresswell (2004) evaluated the effects of potential postfire nutrient inputs on growth by using data from Yellowstone Lake for 4 years before and 4 years after fires that burned approximately 28% of the lake's watershed in 1988. There was evidence that growth had increased for older and larger fish and had declined for younger and smaller fish during the 8-year period; however, there were no statistically significant changes from the long-term trends (1978–1987) that were apparent before the fire (Gresswell 2004). In fact, the results suggested that prior to major effects from the lake trout introduction, annual variations in growth of Yellowstone cutthroat trout were more closely related to changes in population density than to changes in nutrient input. Observed changes in growth rates are consistent with documented alterations (i.e., in population structure and life history variation) that are commonly associated with activities such as angler harvest, hatchery operations, and introduction of nonnative fishes (Gresswell and Varley 1988; Gresswell et al. 1994).

Reproduction

Average size of Yellowstone cutthroat trout spawners varies across the range of this subspecies. Thurow et al. (1988) reported that the mean total length of Yellowstone cutthroat trout spawners in Idaho varied between 300 and 500 mm. Few of the fish that were smaller than 200 mm were mature, and most of the fluvial–adfluvial spawners were 275 mm or larger. In the Yellowstone River (Montana), Clancy (1988) classified fish larger than 300 mm as adults, and spawners from two tributaries to the river varied from 322 to 368 mm in 1988 and 1989 (Byorth 1990). Benson and Bulkley (1963) reported that fish larger than 300 mm were mature in Yellowstone Lake and that most fish less than 250 mm were immature. Data collected between 1985 and 1992 suggested that the mean length of Yellowstone cutthroat trout spawners in tributaries to Yellowstone Lake ranged from 305 to 405 mm (Gresswell et al. 1997). 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. 2003a). Length-at-maturity models were more informative than age-at-maturity models. Length at maturity was positively correlated with stream order and channel width and was negatively correlated with gradient; there were weak associations with conductivity, elevation, mean aspect, and mean summer water temperature. Furthermore, length at maturity was generally greater for migratory fluvial populations than for nonmigratory populations. For example, individuals from the South Fork Snake River matured at 300 mm and 5 years of age. In other migratory and local populations, maturity began at ages 2–3 and at lengths of 100–150 mm. At sites with nonmigratory life histories, most of the 100–250-mm Yellowstone cutthroat trout were mature (Meyer et al. 2003a).

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

Mean age of spawners is also variable. 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). In the Yellowstone River between Corwin Springs and Springdale, Montana, maturity was also estimated to occur at age 3 (Clancy 1988).

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

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. 1997). Males often dominated the early portion of spawning migrations, however, and the proportion of females increased as the spawning migration progressed (USFWS, unpublished data). Between 1945 and 1953, mean male : female ratios for six tributaries to Yellowstone Lake ranged from 0.61:1.00 to 0.74:1.00 (Ball and Cope 1961). Estimates for 13 sample years between 1973 and 1992 at Clear Creek ranged from 0.52:1.00 to 0.75:1.00 (USFWS, unpublished data).

In a study of Yellowstone cutthroat trout populations at 11 sites in southeastern Idaho (Meyer et al. 2003a), the male : female ratio varied from 0.52:1.00 to 2.70:1.00 (n = 29–80), and males were more common than females at eight sites. In that study, a single sample was collected from a 200–400-m section at each site. Berg (1975) and Byorth (1990) found that males were more common early in the spawning migration, but as the migration peaked the male : female ratio approached 1:1.

It is also apparent that angler harvest may affect the male : female ratio. For example, for the first 2 years after angling regulations were changed to catch and release (no harvest) on the Yellowstone River below Yellowstone Lake (1973), male : female ratios were 0.73:1.00 and 0.79:1.00, but between 1976 and 1992 the male : female ratio dropped below 1.06:1.00 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).

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 horribilis* 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%. In Arnica Creek during 1951 and 1952, 28% of Yellowstone cutthroat trout spawners died near spawning sites and an additional 1% 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% (Jones et al. 1985). Instream mortality at Clear Creek increased from 1987 to 1992 (mean = 31%; USFWS, unpublished data).

Mean fecundity of Yellowstone cutthroat trout varies among populations. For example, estimates in the early 1980s were 1,393 eggs/female for the Clear Creek population (Yellowstone Lake; mean length = 394 mm) and 1,577 (mean length = 319 mm) and 2,930 eggs/female (mean length = 518 mm) for the Henrys Lake population (Thurow et al. 1988). Mean fecundity of females collected from the South Fork Snake River (mean length = 377 mm) during the same period was 1,413 eggs/female (Moore and Schill 1984). 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) 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) of Yellowstone cutthroat trout at Clear Creek was similar from the 1950s through the early 1990s (~2,600 eggs/kg), but average fecundity of individual females rose with increases in mean length during that period. As the number of spawners increased in response to changes in angling regulations, population fecundity rose from about 6.2 million eggs during the 1950s to an average of almost 32 million eggs between 1975 and 1992 (Gresswell 1995).

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

In contrast, trampling by cattle may potentially increase mortality of developing embryos and decrease population resiliency in areas where other stressors are threatening population persistence (Peterson et al. 2010).

Eggs generally hatch in 25–49 d (310 accumulated temperature units); 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 that are smaller than 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% within 25 d 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 1–3 years. Similar patterns have been reported for tributaries to Yellowstone Lake (Benson 1960; Gresswell et al. 1997) and the Yellowstone River drainage in Montana (Byorth 1990). Distance from redd to stream mouth may influence the length of time for which fry remain in tributaries to Yellowstone Lake (Welsh 1952), and substantial numbers may remain in some streams through the winter (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

Throughout their range, Yellowstone cutthroat trout have evolved in relatively species-poor fish assemblages. Moreover, only 10 other fish species also occurred above Shoshone Falls after the Pleistocene glaciation (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). On the east side of the continental divide, longnose dace and 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 bairdii*, longnose suckers, white suckers *Catostomus commersonii*, and longnose dace (Clancy 1988).

This relatively simple assemblage of fishes indirectly affected the probability of persistence for Yellowstone cutthroat trout in two important ways. First, the paucity of fish species, especially sport fishes, was viewed by early conservationists as a problem; this belief resulted in the widespread introduction of nonnative fishes and the interbasin transfer of native fishes throughout the historic range of the Yellowstone cutthroat trout. Second, these relatively simple systems provided scant buffering from the competition and predation effects associated with the introduction of nonnative fishes (see Threats).

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 (e.g., bald eagle *Haliaeetus leucocephalus* and grizzly bear) are reported to feed on Yellowstone cutthroat trout (Schullery and Varley 1995). Prior to the illegal introduction of lake trout into Yellowstone Lake, piscivorous avifauna probably had the greatest effect on Yellowstone cutthroat trout in that drainage (Gresswell 1995; Stapp and Hayward 2002a). The size and biomass of fish consumed per day varied among the 20 or more bird species that used 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).

Ward (1922) suggested that American white pelicans alone removed 350,000 Yellowstone cutthroat trout (~105,900 kg) annually during the 1920s (based on population estimates of 500–600 pelicans). Although recent evidence implies that this estimate was excessive, Davenport (1974) found that biomass of Yellowstone cutthroat trout consumed by American white pelicans was at least 34,500 kg (400 pelicans) in 1973 and 16,800 kg (195 pelicans) in 1974. She concluded that interannual variation in consumption was related to the fluctuation in reproductive success of American white pelicans in the southern part of the lake (Davenport 1974). American white pelicans were common on the Yellowstone River below Yellowstone Lake in the early 1990s, 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 American white pelicans observed in the river.

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

Other piscivorous birds include the 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 *Bucephala 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 Yellowstone cutthroat trout spawners and larval offspring. With the possible exception of the double-crested cormorant, these birds primarily focus on fish in shallow portions of the littoral area and tributaries where the Yellowstone cutthroat trout is the most common fish (Schullery and Varley 1995; McEneaney 2002).

Model predictions suggest that mammalian predators historically consumed about 7% of the Yellowstone cutthroat trout population in Yellowstone Lake each year (Stapp and Hayward 2002a). Yellowstone cutthroat trout are especially vulnerable to predation during the spawning period, and they are seasonally important in the diets of grizzly bears in the lake area (Mealey 1980; Mattson and Reinhart 1995; Haroldson et al. 2005). Dumps had become the primary feeding areas for grizzly bears by the 1960s, and thus 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 1970s may have had indirect positive effects on grizzly bears, and the number of streams frequented by grizzly bears increased from 1974–1975 to 1985–1987 (Reinhart and Mattson 1990). After the introduction of lake trout, however, numbers of spawning Yellowstone cutthroat trout and indices of grizzly bear use declined on streams near the developments of Grant Village and Lake Village from 1990 to 1995 (Reinhart et al. 2001). Haroldson et al. (2005) documented lakewide declines in the number of Yellowstone cutthroat trout spawners between 1989 and 2000.

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

Perhaps the most significant effect of predation on the Yellowstone cutthroat trout has occurred in Yellowstone Lake since the introduction of lake trout. Yellowstone 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 during 1996–1999, Ruzycki et al. (2003) reported that lake trout commonly consumed Yellowstone cutthroat trout of lengths equal to 27–33% of predator body length, and it was estimated that each lake trout ingested an average of 41 Yellowstone cutthroat trout annually. Expanded results suggested that about 15.1 metric tons of Yellowstone cutthroat trout or 129,000 individuals (about 14% of the annual Yellowstone cutthroat trout production) were consumed by lake trout in 1996 (Ruzycki et al. 2003). By 2004, the decline in Yellowstone cutthroat trout had resulted in a major shift in the structure of the zooplankton and phytoplankton communities in Yellowstone Lake (Tronstad et al. 2010).

Since 1994, when lake trout were first discovered in Yellowstone Lake, the annual spawning migration of Yellowstone cutthroat trout into Yellowstone Lake tributaries has declined precipitously (Gresswell 2009) and relative abundance estimates from annual monitoring with gill nets are among the lowest since the monitoring program began in 1969 (Gresswell et al. 1994). These declines in Yellowstone cutthroat trout abundance may substantially affect other predators throughout the Yellowstone Lake ecosystem (Varley and Schullery 1995; Stapp and Hayward 2002b; Crait and Ben-David 2006). For example, American white pelicans have maintained their 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.G., 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 grizzly bears (2,226 fish annually; Felicetti et al. 2004) are less than 2% of the estimated number consumed by lake trout in the 1990s (Ruzycki et al. 2003; Felicetti et al. 2004).

Published accounts that document predation on Yellowstone cutthroat trout in other parts of the historical range were not located, but Yellowstone cutthroat trout are presumably important to avian and terrestrial predators wherever population abundance is sufficient. Predation by nonnative salmonids (e.g., brook trout and brown trout) is often suggested as a mechanism driving population extirpation for all subspecies of cutthroat trout, but direct evidence of this 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 Yellowstone cutthroat trout in Jackson Lake (Grand Teton National Park) and Heart Lake historically preyed on other fishes with which they evolved; therefore, the effects of introduced lake trout on these native assemblages may not have been as extreme.

Competition

Competition is often suggested as a regulating factor influencing salmonid population abundance, but direct competition is sometimes difficult to document. This is especially evident in studies of competition between salmonid and nonsalmonid fishes. For example, there was no evidence that the introduction of the 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 suckers *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 interactions at the individual level rather than population-level responses (Peterson and Fausch 2003). Furthermore, the outcome varies. In the headwaters of the Madison River, westslope cutthroat trout and fluvial Arctic grayling *Thymallus arcticus* were extirpated after the introduction of nonnative 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 with westslope cutthroat trout in Montana (Wang and White 1994). In some Idaho streams, Yellowstone cutthroat trout have persisted in areas occupied by introduced brown trout and brook trout as long as habitat has not been degraded and angler harvest is minimal (Thurow et al. 1988). However, because the outcome of competitive interactions can be affected by abiotic conditions such as water temperature (Fausch 1989; Dunson and Travis 1991; Shepard 2004), these relationships may not persist if water temperatures increase due to climate change.

Cutthroat trout may be less likely to coexist with brook trout than with other nonnative salmonids (Griffith 1988); in Yellowstone National Park, Yellowstone cutthroat trout seldom occur in areas where brook trout have been introduced (Varley and Gresswell 1988). Among the mechanisms for displacement, competitive exclusion has been cited most frequently, and niche overlap may be greater between Yellowstone cutthroat trout and brook trout than between 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 appear to be 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.

Peterson et al. (2004) documented that although brook trout invasion does not always result in complete extirpation of native cutthroat trout throughout watersheds, this nonnative invader is effective in headwater streams of the central Rocky Mountains. Apparently, brook trout can recruit and survive as well as or better than native greenback cutthroat trout *O. clarkii stomias* and Colorado River cutthroat trout *O. clarkii pleuriticus*, and at mid-elevation sites the native cutthroat trout are often replaced through suppression of vulnerable juvenile life stages (Peterson et al. 2004). At colder, high-elevation sites, however, water temperature limits cutthroat trout reproduction in areas where the number of accumulated temperature units is less than 900 during the summer (Coleman and Fausch 2007a). Apparently, temperature-related energy deficits lead to a recruitment bottleneck 4–6 weeks after swim-up (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 nonnative species. Few studies have directly addressed this hypothesis; however, Sestrich et al. (2011) recently reported that where connectivity in stream networks was high, populations of westslope cutthroat trout and bull trout *Salvelinus confluentus* were not extirpated after wildfire disturbance. In fact, these native fishes recovered more quickly than nonnative trout in most watersheds.

Peterson and Fausch (2003) argued that interspecific interactions, net emigration, disease introduced by invading species, or some combination of these factors are the primary direct mechanisms resulting in declines in native species abundance after invasion by nonnative salmonids. Additionally, abundance of the invading species must increase through reproduction, high survival, net immigration, or a combination of these factors (Peterson and Fausch 2003). It appears that biotic interactions negatively affect native cutthroat trout even when habitat factors are favorable (Quist and Hubert 2005). Although 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 (Gresswell 1988; Van Kirk and Benjamin 2001; Winters et al. 2004b).

Disease and Parasites

Prior to the late 1980s, enzootic levels of disease in naturally reproducing populations of Yellowstone cutthroat trout were poorly documented. *Aeromonas salmonicida*, the causative agent of furunculosis, had been isolated from spawners in the Yellowstone River below Yellowstone Lake (USFWS, unpublished data), and MacConnell and Peterson (1992) reported the occurrence of proliferative kidney disease in a feral population of cutthroat trout in a remote Montana reservoir. Since that time, whirling disease, which is caused by the exotic parasite *M. cerebralis*, has been found in the native range of the Yellowstone cutthroat trout (Burckhardt and Hubert 2005), 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 spawners 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, Montana State University, unpublished data).

The life cycle of *M. cerebralis* includes two intermediate spore stages (triactinomyxons and myxospores) and two obligate hosts (an oligochaete *Tubifex tubifex* and a salmonid belonging to one of the various susceptible species; Kerans et al. 2005). A substantial amount of information has emerged in the last decade concerning differences in fish host susceptibility related to species, sex, and age (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. 2005); and diagnostics (Andree et al. 1998).

Yellowstone cutthroat trout exhibit a strong disease response to *M. cerebralis* exposure (Hiner and Moffitt 2001; Wagner et al. 2002). Moreover, habitat characteristics influence infection rates; Burckhardt and Hubert (2005) 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 main stem, and site elevation were negatively correlated with infection in that study (Burckhardt and Hubert 2005).

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). In the 1950s, more than 10,000 Yellowstone cutthroat trout from tributaries to Yellowstone Lake were examined for parasites, and 55–60% of these fish were found to have parasites (Cope 1958). In other portions of the current range of Yellowstone cutthroat trout, the extent of parasite occurrence in populations is not well documented (Woodbury 1934; Bangham 1951; Hoffman 1967).

One of the most infamous of the parasites is the tapeworm found in Yellowstone Lake. Originally identified as *Diphyllobothrium cordiceps* (Heckmann and Ching 1987), taxonomic work in the 1980s yielded two species (*Diphyllobothrium ditremum* and *D. dendriticum*) instead of one (Otto and Heckmann 1984). The American white pelican is a definitive host of these tapeworms (Linton 1891), and there was a plan in the 1920s to destroy American white pelican eggs on the rookery in an effort to reduce the incidence of tapeworms by controlling the bird population (Varley and Schullery 1998). Infestation rates in Yellowstone cutthroat trout can be high (46–100%; Woodbury 1934; Bangham 1951; 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. Yellowstone cutthroat trout may harbor more than 400 plerocercoids (tapeworm larval stage; Heckmann 1971), but activity levels appear to be unchanged in at least some individuals with a high level of tapeworm infestation (Post 1971).

To anglers, the primary concern of tapeworm infestation is esthetic (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 the parasitized fish. This was a major issue in the late 1950s, when harvest limits on Yellowstone Lake were 3 fish/d; however, by the late 1970s disposal rates under a two-fish, 330-mm maximum size limit for Yellowstone cutthroat trout were very low. Apparently, infection rate is lower in younger Yellowstone cutthroat trout that are harvested under regulations stipulating the release of larger individuals (Gresswell 1995).

An eye fluke *Diplostomum baeri bucculentum* occurs quite commonly in Yellowstone cutthroat trout 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 disease's effect on visual acuity of Yellowstone cutthroat trout (Heckmann and Ching 1987). Severe infections may compromise the ability of an individual to feed, and ultimately growth may be affected.

Another parasite-mediated disease, black spot disease, is not broadly spread across the range of Yellowstone cutthroat trout but is locally common in the Teton River of eastern Idaho and western Wyoming (Shrader and Brenden 2004). The disease has also been reported in other streams of western Wyoming (Bangham 1951). Metacercariae of digenetic (multiple hosts) trematode parasites from at least five genera are the causal agents of black spot disease; a fish-eating bird (e.g., a kingfisher, gull, or heron) acts as the primary host (Steedman 1991). Adult worms inhabit the gut of the bird. Eggs enter the water in bird fecal matter, and after hatching the miracidia infect the first intermediate host, a snail belonging to any of several species. Subsequently, sporocysts formed in the snail develop into cercariae that infect the second intermediate host, a fish. The cercariae burrow directly into the skin of the fish and encyst as metacercariae or larvae (Steedman 1991). In the fish, the cyst is engulfed with a dark melanin pigment that produces the 1–2-mm-diameter black spots on the fins, skin, and gills (Shrader and Brenden 2004). The eye of a heavily infected fish may bulge out of the socket, creating a condition called "popeye" (Shrader and Brenden 2004). The life cycle of the trematode is completed when the infected fish is eaten by a bird.

THREATS

Nonnative and Invasive Species

Nonnative fishes, both exotic species (naturally occurring outside the North American continent) and native North American species that are introduced via interbasin transfers, collectively constitute the primary threat to persistence of Yellowstone cutthroat trout (Varley and Gresswell 1988; Kruse et al. 2000). Although interbasin transfers of fish by humans have probably occurred periodically through history, major continental-scale introductions of nonnative fishes have increased (frequently in conjunction with official government programs) since the latter part of the 19th century (Behnke 1992; Varley and Schullery 1998; Rahel 2002). Moreover, natural movement of nonnative fishes from areas where they have become established is common (Peterson and Fausch 2003).

Barriers to movement may restrict access by nonnative species; however, the probability of interbasin transfer, either legally or illegally, is also a significant problem (Peterson and Fausch 2003). In Montana alone, 375 unauthorized introductions of fishes were documented through the mid-1990s, and 45 different species were illegally introduced into 224 different waters (Vashro 1995).

Hybridization.—For the Yellowstone cutthroat trout, hybridization resulting from introductions of rainbow trout and nonnative 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 rainbow trout × Yellowstone cutthroat trout hybrids are developmentally successful, progeny may appear to be morphologically and meristically intermediate between parental types or may be virtually identical to a single parental type (Ferguson et al. 1985). Therefore, it is difficult to verify genetic integrity based on morphological data alone, and nuclear allozymes, mtDNA haplotypes, and nuclear DNA have proven to be 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 from 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. In areas where rainbow trout have been stocked within the historical range of Yellowstone cutthroat trout in Montana, there are hybrid populations of the two species (Hanzel 1959). Allendorf and Leary (1988) analyzed 16 samples of Yellowstone cutthroat trout from tributaries to the Yellowstone River in Montana and reported that half of the samples represented genetically unaltered populations; because sample sites were selected without prior knowledge of genetic integrity, these findings may be a realistic representation of hybridization in the Yellowstone River drainage in the 1980s. Kruse et al. (2000) reported that only 26% of the 104 Wyoming trout streams still supported genetically pure Yellowstone cutthroat trout, and 21 (78%) of the stream segments with genetically pure populations contained no other fish species.

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). A recent study of 73 radio-tagged Yellowstone cutthroat trout, rainbow trout, and their 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 low (DeRito et al. 2010). 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 97.5–100% Yellowstone cutthroat trout; rainbow trout introgression was only observed in one of the aggregations (DeRito et al. 2010).

Unfortunately, after 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, Yellowstone cutthroat trout, and hybrids. Overlap in the 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 (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, then temporal overlap with Yellowstone cutthroat trout might be higher for hybrids than for rainbow trout parent stocks (Allendorf et al. 2004).

Conservation efforts implemented on the South Fork Snake River (High 2010) provide an important case study of the current management efforts to protect Yellowstone cutthroat trout from the threats of hybridization. Beginning in 2004, a multifaceted strategy was initiated to (1) remove rainbow trout and rainbow trout × Yellowstone cutthroat trout hybrids entering four primary Yellowstone cutthroat trout spawning streams, (2) alter discharge patterns below Palisades Dam to reduce rainbow trout and hybrid reproduction success in the main-stem river, and (3) reduce the abundance of rainbow trout and hybrids through targeted angler harvest. To date, the plan has had mixed results, and rainbow trout and hybrids continue to increase (High 2010). Trapping efficiency has been variable, and irrigation demands, snowpack variation, and reservoir storage requirements make it difficult to successfully mimic natural patterns of discharge on an annual basis. Angler harvest of rainbow trout and hybrids has risen, but removal remains below levels that are necessary to negatively affect the invaders (High 2010). Results of this program underscore the difficulty of restoring the integrity of large rivers after the introduction of nonnative fishes, especially when they successfully interbreed with valued native fishes.

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 in Yellowstone cutthroat trout after introduction or invasion of nonnative fishes. Kruse et al. (2000) suggested that nonnative fishes were the principal reason that Yellowstone cutthroat trout declined in the Greybull, North Fork Shoshone, and South Fork Shoshone rivers. Furthermore, there was no evidence that habitat changes had substantially influenced the remaining populations (Kruse et al. 2000). Moreover, lack of habitat segregation among brook trout, rainbow trout, and Yellowstone 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 and Wyoming), Quist and Hubert (2005) found that when brown trout and brook trout densities were low, Yellowstone cutthroat trout density was highly variable and more closely related to habitat characteristics. Yellowstone 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 on Yellowstone cutthroat trout have been documented over the past decade in Yellowstone Lake, and current evidence suggests that nonnative 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), Yellowstone cutthroat trout of lengths equal to approximately 27–33% of lake trout body length are vulnerable to predation, and juveniles are especially vulnerable. Effects of predation have not been studied extensively in other portions of the subspecies' 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 displace native cutthroat trout (Kruse et al. 2000; Quist and Hubert 2005)

Although nonnative 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% of all juvenile and adult Yellowstone cutthroat trout in Yellowstone Lake are infected with *M. 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 Yellowstone Lake, but samples from 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 more than 90% 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).

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 the subspecies' distribution and abundance (Thurow et al. 1997; Van Kirk and Benjamin 2001; Winters et al. 2004b). 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. 2004a), and these perturbations are especially prevalent in portions of the historical range that occur on nonfederal 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; Elle and Gamblin 1993; Van Kirk and Benjamin 2001). Furthermore, dams have isolated migratory fishes from spawning and rearing areas in the Blackfoot, Portneuf, South Fork Snake, Teton, Henrys Fork Snake, and main-stem Snake rivers (Thurow et al. 1988). Van Kirk and Benjamin (2001) reported a direct 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 (Thurow et al. 1988; IDFG 2007), and there are thousands located in the current range of the subspecies (Winters et al. 2004b; IDFG 2007). In many cases, spawning habitat for Yellowstone cutthroat trout in tributaries is lost where water diversion occurs annually (Byorth 1990). In the Yellowstone River (Montana), the population density of Yellowstone cutthroat trout is generally greatest in the vicinity of tributaries that support spawning migrations. In Idaho, irrigation removals seriously affect Willow Creek and the Blackfoot, Henrys Fork Snake, Portneuf, Raft, Teton, and main-stem Snake rivers (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 (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. 2004b).

Habitat fragmentation can negatively affect the persistence of Yellowstone cutthroat trout 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 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 was altered by habitat fragmentation (Cegelski et al. 2006). Furthermore, fragmentation can destroy critical dispersal pathways among populations, preventing repopulation after 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 by 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).

Fish movement barriers 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 contribute to interfere with fish passage (Winters et al. 2004a). 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. 2004a; IDFG 2007). 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 (Jones et al. 1986). In many portions of the subspecies' current range, reach- or site-level analyses to assess the influence of culverts and other road-related issues on Yellowstone cutthroat trout populations have not been conducted (Winters et al. 2004b).

Effects of excessive livestock grazing on riparian habitats are well documented (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, Montana Department of Fish, Wildlife, and Parks, personal communication). In Idaho, however, intensive livestock grazing has caused degradation of riparian areas and subsequent streambank 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) argued that (1) there was no evidence that habitat alteration had significantly affected the remaining populations of Yellowstone cutthroat trout in northwestern Wyoming and (2) nonnative fishes appeared to be the primary reason for declining populations. Winters et al. (2004a) argued that livestock grazing is only one factor affecting the condition of riparian habitats and that roads, recreational activities, grazing by wild ungulates, 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 evidence of local extirpations. For example, Thurow et al. (1988) reported increased sedimentation associated with phosphate mines in the Blackfoot River drainage (Idaho). Furthermore, recent research by Van Kirk and Hill (2006) suggests that selenium concentrations in Yellowstone cutthroat 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 1960s (Jones et al. 1982). During that period, fish populations were depressed downstream in Yellowstone National Park and anglers had minimal success. After reclamation of the tailings, the 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 the 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 cadmium, copper, and zinc 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 the current negative effects of nonnative aquatic species and habitat degradation. Mean air temperatures have increased by approximately 0.6°C globally during the past 100 years (IPCC 2001; Walther et al. 2002). There have been two primary periods of warming—from 1910 to 1945 and from 1976 to the 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 the last 1,000 years (IPCC 2001; Walther et al. 2002).

Air temperature is expected to continue to warm globally from 1.4°C to 5.8°C during the 21st century (IPCC 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 coldwater species are expected to shift northward in latitude and upward 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 7.5–43.3% for each 1–5°C increase in temperature. These estimates include minor increases in suitable habitats at high elevations as temperatures increase. Lake habitats for coldwater fish could decline up to 45% as temperatures increase. Shallow lakes may desiccate completely, and water depth of deeper lakes will probably decrease. The greatest negative effects will most likely be in lakes of moderate depth (≤13-m maximum depth; Stefan et al. 2001).

Most predictions of future climate have been based on simple, single-variable models focused on temperature at the global scale, and the models do not account for the interaction of physical variables that will be affected by climate change. 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 nonadditive interactions between hydrologic and temperature effects (Jager et al. 1999). Accurately predicting such interactions will be difficult, however, because climate model projections of future precipitation are more variable and uncertain than projections of temperature.

In an effort to move beyond the single-factor analyses, Haak et al. (2010) assessed the effects of four potentially detrimental factors related to climate change (i.e., warmer summer temperatures, increased winter flooding, increased wildfires, and drought) on 10 salmonid taxa, including Yellowstone cutthroat trout. Drought was identified as the greatest risk factor for the core conservation populations of Yellowstone cutthroat trout. Wildfire and winter flooding were also high risk factors for the subspecies, whereas increasing summer temperature was a low risk for most populations. In fact, core conservation populations in high-elevation streams around Yellowstone Lake and the upper Snake River and Wind River headwaters were rated as low risk for all of the climate change factors (Haak et al. 2010).

Global model predictions may be useful for obtaining a 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 that some existing climate states may disappear completely (Williams et al. 2007). As models become more complex and refined, local land management history and species pool are other factors that should be considered because habitat fragmentation and nonnative species have reduced the capacity of aquatic systems to respond to the effects of disturbances such as climate change (sensu Warren and Liss 1980).

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 the 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 reside in near proximity may change dramatically under altered climate scenarios, and these interactions have not been investigated.

Angler Harvest

Substantial declines in population abundance of Yellowstone cutthroat trout have been related to overharvest throughout the historical range of the subspecies (Binns 1977; Gresswell and Varley 1988). Vulnerability of Yellowstone cutthroat trout to angling is high. In fact, in the early 1980s, individuals in the Yellowstone River (Yellowstone National Park) were captured an average of 9.7 times during the 108-d 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 and Varley 1988; Gresswell 1995; Gresswell and Liss 1995).

In some cases where nonnative salmonids are sympatric with Yellowstone cutthroat trout, angler harvest may contribute to species replacement and eventual extirpation (Griffith 1988). Because nonnative salmonids are usually less vulnerable to angling than Yellowstone cutthroat trout (Schill et al. 1986; Gresswell and Liss 1995), unequal mortality due to angling could contribute to the eventual dominance of nonnative fishes. If another salmonid displaces cutthroat trout, the situation is often irreversible, especially in larger streams and lakes (Moyle and Vondracek 1985; Kolar et al. 2010).

All state, federal, and tribal agencies that have management authority for Yellowstone cutthroat trout currently manage the subspecies as a sport fish (WGFD 2005; IDFG 2007; 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 and Harding 1997). Furthermore, as concern for the 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.

FUTURE MANAGEMENT OF THE YELLOWSTONE CUTTHROAT TROUT

Throughout the 20th century, the distribution and abundance of Yellowstone cutthroat trout declined and population 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 many of these remote areas public ownership (in the form of national parks and wilderness areas) has provided habitat protection that is lacking in low-elevation portions of the range. For example, state and federal agencies administer over 70% of the lands that support Yellowstone cutthroat trout (i.e., current distribution, conservation populations, and core populations). Historically, 51% of the lands supporting Yellowstone cutthroat trout were private lands, but currently only about 20% of the current distribution is found on private lands (May et al. 2007).

Management actions (e.g., special regulations, riparian fencing, culvert replacement, bank stabilization, instream habitat restoration, population restoration or expansion, and chemical removal of competing or hybridizing species) initiated in the past several decades have stabilized—and in some cases extended—the distribution of Yellowstone cutthroat trout. Despite the presence of numerous populations, however, most of the genetically unaltered assemblages (core conservation populations) are found in fragmented habitats within headwater streams, where abundance is low (May et al. 2007). Recent introductions of nonnative species and persistent drought in the Northern Rocky Mountains have caused increased concern about many populations that had previously been deemed secure. Current projections suggest that changes in climate and the concomitant shifts in timing and availability of water will continue to exacerbate the probability that the Yellowstone cutthroat trout's range in the region will decline. As water temperatures increase, current Yellowstone cutthroat trout habitat may become more conducive for nonnative 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 into lower portions of the watershed, where nonnative salmonids are more prevalent. Furthermore, the potential for upstream movement may be limited by habitat alterations (e.g., culverts and diversions) or by the presence of nonnative brook trout.

Current estimates of the status and distribution of Yellowstone cutthroat trout suggest that it will be impossible to restore the subspecies to 100% of its historical range. Furthermore, the proportion of the range that supports healthy, secure core conservation populations is apparently low (May et al. 2007), and given the range of potential factors that are negatively affecting Yellowstone cutthroat trout populations, the persistence of core populations is not certain. Management 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.

Protection of the remaining strongholds of genetically unaltered individuals is probably the most important management priority (Frissell 1997). As was noted above, once a population has been altered, the restoration of that population is uncertain. Preventing the invasion of nonnative fishes by either natural pathways (migration from previously established populations) or anthropogenic pathways (transplanting) is critical. To avoid introgression with nonnative taxa (including Yellowstone cutthroat trout from other portions of the historical range), the stocking of nonnative fishes to support recreational angling in streams and lakes should be precluded. In cases where nonnative fishes occur in the watershed, physical isolation of the remaining Yellowstone cutthroat trout by barrier construction may be required (Fausch et al. 2006). Alternatively, it may be possible to remove the nonnative fishes by either physical or chemical means (Finlayson et al. 2005; Peterson et al. 2008a; Kolar et al. 2010). It is also important to consider restricting human activities that would directly (e.g., pollution) or indirectly (e.g., habitat degradation) compromise these populations of Yellowstone cutthroat trout.

Although it is important to prevent further degradation in areas that support core conservation populations, efforts focused on population enhancement are critical. Perhaps the most crucial management action in many of these systems is the removal of nonnative salmonids where they co-occur with Yellowstone cutthroat trout. Current evidence suggests that taxa with the ability to hybridize with Yellowstone cutthroat trout (e.g., rainbow trout and other cutthroat trout subspecies) pose the greatest threat to persistence of this subspecies (May et al. 2007); to reduce this threat, the removal of nonnative fishes from these systems should be a priority. Where hybrids occur, removal may be necessary to improve genetic integrity. As noted above, either physical or chemical means may be used, and habitat conditions generally dictate which method is appropriate.

Specific habitat management activities focused on improving riparian and stream channel conditions can be useful for improving habitat conditions (Winters et al. 2004a) for core conservation populations of Yellowstone cutthroat trout. Where possible, the reconnection of 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, it will be necessary to remove nonnative species before disparate portions of a stream network can be reconnected by eliminating anthropogenic barriers to fish movement (e.g., culverts and water diversion structures). This is especially important in systems where barrier removal would allow nonnative fishes to access habitat that is currently occupied by allopatric assemblages of Yellowstone cutthroat trout. Until removal of nonnative species occurs, connectivity may require human translocations to maintain a sufficient effective population size (Fausch et al. 2006; Peterson et al. 2008b).

Replication of core conservation populations would involve introducing Yellowstone cutthroat trout into a watershed where they did not occur historically because of passage barriers. This is another strategy that may improve the probability of the subspecies' persistence because many of the remaining core conservation populations occur in nonnetworked systems that may be vulnerable to catastrophic disturbance events. Although there may be ethical issues associated with this type of management activity, the potential benefits to the Yellowstone cutthroat trout's persistence may substantially outweigh the negative effects on native invertebrate communities. For example, fishless headwater streams often comprise over 60–80% of the cumulative channel length in mountainous areas (Schumm 1956; Shreve 1969), and redundancy of invertebrate communities is often high. Despite the fact that many of the fishless streams in the western United States occur in wilderness areas, current management policies restrict the introduction of any fish into previously fishless waters (except where stocking preceded wilderness designation; USFS et al. 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 (Rinne and Turner 1991). Total extirpation of introduced nonnative 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 nonnative fishes is often low, and most projects in streams require two or more piscicide applications (Finlayson et al. 2002). In addition, social issues sometimes engender legal challenges to renovation projects (Quist and Hubert 2004; Finlayson et al. 2005). Habitat degradation can be severe where Yellowstone cutthroat trout have been extirpated, and restoration may require decades or centuries (Frissell 1997). Because of the extensive amount of time necessary to observe the anticipated results, maintaining support for such projects is often difficult.

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 nonnative fishes have not invaded the upstream portions of a watershed. Removal of passage barriers (natural and anthropogenic) may increase the probability of persistence and allow for the expression of life histories (e.g., migratory life history types) that were suppressed by such barriers; however, in many cases, providing access to nonnative fishes may be a more significant short-term threat (Peterson et al. 2008b). Purposely isolating populations by the construction of barriers may increase the short-term probability of persistence, but in some cases this alternative has negative long-term consequences. Fausch et al. (2006) proposed a framework for decision making based on four questions relating to (1) the conservation value of the population of interest, (2) the population's vulnerability to invasion and displacement, (3) the probability of persistence if the population is isolated, and (4) the population's relative priority among the multiple populations that may be at risk. In an effort to develop a more formal decision support tool for making management decisions associated with this issue, Peterson et al. (2008b) designed 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. When this tool was applied to native westslope cutthroat trout and nonnative brook trout in western Montana, Peterson et al. (2008b) found that habitat quality and size of the target stream network and demographic relationships within and among populations were the major factors influencing decisions between isolation and invasion.

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. 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 rangewide strategy because identification and testing will need to be coordinated across a variety of state and federal agencies and for public and private lands.

An integrated monitoring plan represents a second vital component of management that requires cooperation of state and federal management agencies 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 would expand the scope of inference associated with future assessments to the entire range of the subspecies. Because trend detection is the ultimate goal of most assessments, a design that includes a network of probabilistically chosen sites would ensure that monitoring is consistent through time. Additionally, an independent effectiveness monitoring program would provide necessary evaluation for habitat improvement, nonnative species removal, and Yellowstone cutthroat trout introduction or reintroduction projects.

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