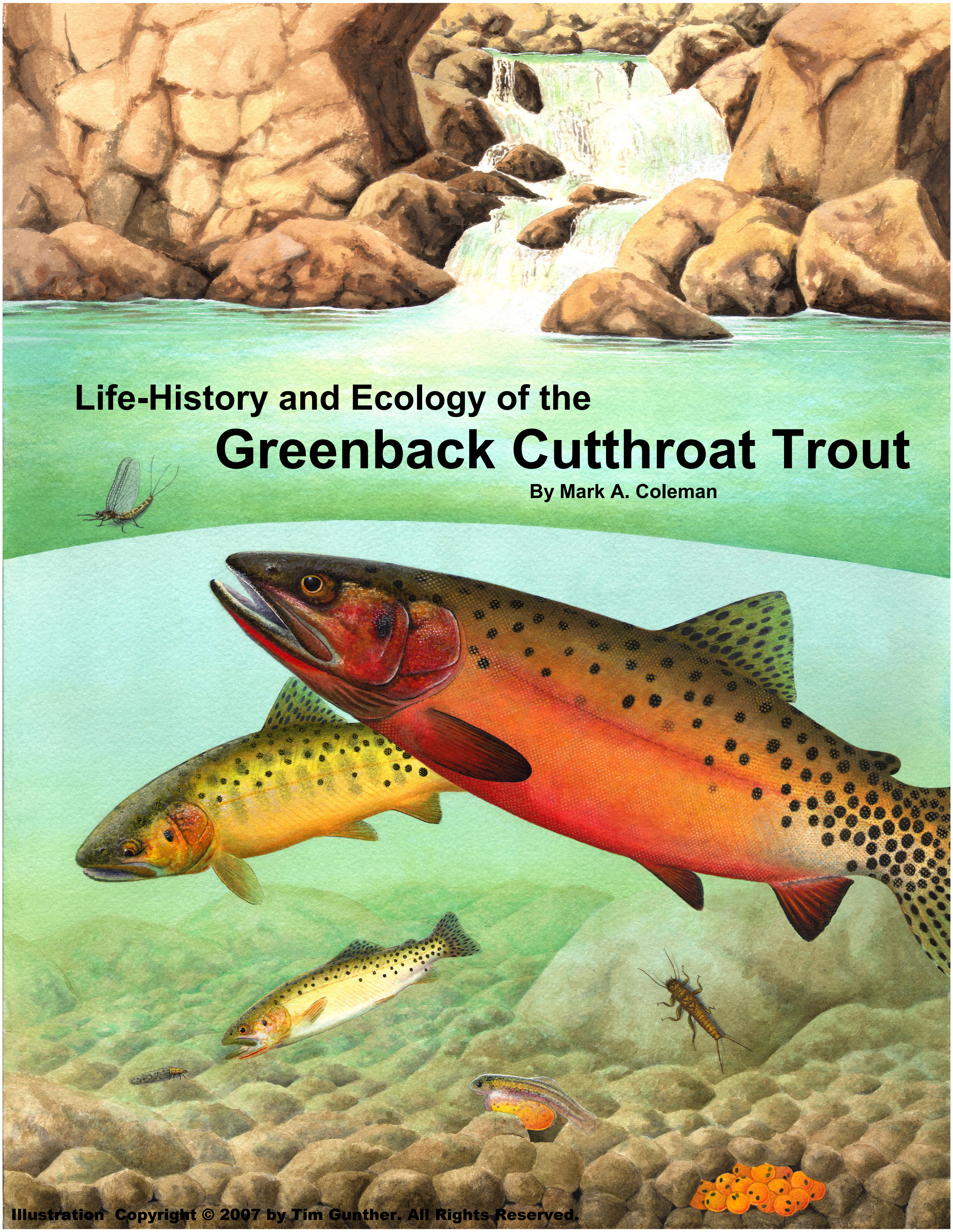
Life-History and Ecology of the

Greenback Cutthroat Trout

By Mark A. Coleman



Natural Heritage Program COLORADO

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West Creek Falls is a natural barrier to upstream migration.

INTRODUCTION

The greenback cutthroat trout is one of four cutthroat trout subspecies native to Colorado, one of which (the yellowfin cutthroat) is assumed to be extinct. The only salmonid native to the South Platte and Arkansas River basins, the greenback cutthroat trout was threatened by habitat loss, unregulated fishing, and invasions by introduced nonnative salmonids by the early 1900's, and was thought to be extinct by 1937. However, two pure populations were discovered in the 1950's and 60's, with the subspecies listed as "Endangered" under the Endangered Species Act when enacted in 1973. In 1978, their status was changed to "Threatened" with discovery of additional historical populations and successful translocations above barriers to upstream migration that prevent invasion by nonnative salmonids. Management and recovery had resulted in 20 stable populations by 1998 (USFWS 1998). The greenback cutthroat trout was believed to be poised for delisting by 2006, when efforts to prepare a long-range management plan for the subspecies began.

This report summarizes what is known, or can be gleaned, from research and recorded observations on the life-history and ecology of greenback cutthroat trout. It is organized into four major interrelated sections that review Habitat Requirements, Life-History, Population Ecology, and Community Ecology. Each of these is further subdivided into topics to organize the information presented in meaningful ways, as the report is intended to be adapted for use in the final version of the greenback cutthroat trout long-range management plan. An effort has been made to focus as much as possible on results from studies and observations specifically on greenback cutthroat trout, but in places the greenback-specific information is supplemented with information on other salmonids that are either closely related or have ecological similarities to greenback cutthroat trout. When results from studies on other salmonids were included, it was noted, and further research to fill gaps in the collective knowledge of greenback cutthroat trout life-history and ecology was recommended.

HABITAT REQUIREMENTS

Suitable habitat for self-sustaining salmonid populations must contain sufficient physical complexity to meet the requirements of all life-history stages, from embryo to adult. In this regard, the habitat requirements of greenback cutthroat trout are similar to those of other salmonids confined to fresh waters. Available physical habitats must provide temperatures within the range tolerated by the fish, spawning habitat, small backwater or shallow pocket habitats for newly emerged fry to find prey and refuge from the stream's current, and pool habitat for overwintering of fry and adults.

The turbulent habitat of the greenback cutthroat trout .

Habitats that provide adequate complexity are also generally productive and provide a food base of terrestrial and aquatic invertebrates with the range of sizes needed to sustain fish at each life stage. The water quality must also be suitable, having a tolerable pH and containing low levels of contaminants such as heavy metals and other substances which interfere with physiology and development and threaten the viability of populations.

Elevation

The original elevational distribution of greenback cutthroat trout is unknown, but the upper and lower elevation limits at which greenback cutthroat trout can establish reproducing populations can be estimated based on the results of experimental stockings in both high and low-elevation lakes, and from the historical record. At 3,402 m elevation, the Upper Hutcheson Lake greenback cutthroat trout population is the highest known. Research stocking in other high elevation lakes has resulted in mixed success. For example, greenback cutthroat trout stocked in Lake Odessa (3,048 m) spawned and established a reproducing population, whereas greenback cutthroat trout stocked in Crystal Lake (3,511 m) do not appear to be reproducing at a rate sufficient to maintain this population.

Based on the known historic presence of greenback cutthroat trout in headwaters of both the South Platte and Cache la Poudre River basins, at one time the lower elevational range of greenback cutthroat trout may have extended down to 1,420 m to the confluence of the South Platte and Cache la Poudre rivers near present day Greeley, Colorado (Behnke 1992, 2002). Indeed, greenback cutthroat trout stocked in a low elevation lake (1,889 m) at Fort Carson, Colorado, survived and reached sizes of up to 2.0 kg.

Physical and thermal requirements

Stable and reproducing populations are rarely found above timberline, and the preponderance of evidence suggests that various physical factors, including temperature and habitat structure, constrain the upper elevation limits for greenback cutthroat trout today (USFWS 1998; Harig and Fausch 2002; Coleman and Fausch in press a). Field studies have indicated that temperature and physical habitat characteristics in stream segments at multiple scales are all related to greenback cutthroat trout abundance or the probability of establishing stable populations during recovery efforts (Harig and Fausch 2002). In 27 translocated or reintroduced greenback and Rio Grande cutthroat trout populations, one field study indicated that cold summer temperatures and the number and width of deep pools were correlated with fish abundance at the stream scale (Harig and Fausch 2002), while at a larger scale watershed area was also correlated with fish abundance. Further, Young et al (2005) found that occupied stream length was positively correlated with electrofishing abundance estimates for 31 stream populations of greenback and Colorado River cutthroat trout.

Specific threshold values for habitat characteristics derived from correlative studies like these should be regarded with caution, and not applied as "rules of thumb" because some self-sustaining populations occur in streams that fail to meet some or all of the criteria derived from these studies. Furthermore, management of greenback cutthroat trout can be difficult at lower elevation habitats due to complexity of habitat, water management operations, or presence of structures that prevent successful elimination of non-native salmonids. Although these lower elevation habitats provide the benefits of warmer temperatures and preferred large river habitats relative to headwater streams, other factors often prevent their use for recovery of greenback cutthroat trout. Management for the species is therefore "sandwiched" between lower and upper elevations.

Regardless, the studies described above provide valuable tools for identifying habitats that are probably suitable, probably unsuitable, or may require further investigation to judge suitability. For example, based on the above studies, stream segments that have a watershed area of at least 14.7 km^2, a minimum occupied length of between 2.9 and 3.8 km, mean July temperatures > 7.8ºC, mean bankfull pool width > 3.4 m, and > 69 pools more than 30 cm in residual depth can be assumed to provide sufficient habitat to sustain greenback cutthroat trout populations. Streams that fail to meet most of these criteria can most likely be ruled out as suitable sites for translocations. However, streams that fall short in only one or a few of these criteria should not be ruled out before more detailed assessments have been conducted.

Environmental temperature is a variable that influences nearly every physiological and ecological process necessary for survival of all salmonids. Where habitat is marginal due to cold temperatures and the short growing seasons typical in high elevation streams and lakes, greenback cutthroat trout and other cutthroat trout subspecies that spawn in the spring may not be able to incubate successfully, or grow large enough to insure survival over their first winter (Coleman and Fausch in press a, in press b). In a two-year laboratory study, Colorado River cutthroat trout survived poorly through the start of their first winter in temperature regimes in which fewer than 800 degree-days accumulated between spawning and the start of winter (Coleman and Fausch in press a). Growing season degree-days can be estimated by summing the average daily temperatures during the period each year when temperatures are suitable for growth (e.g., 30 days × 10ºC average daily temperature = 300 degree-days).

In a companion field study, young-of-year greenback or Colorado River cutthroat trout fry densities were very low in stream reaches with fewer than 800 growing season degree-days and

Adult greenback cutthroat trout during spawning season.

fry length was < 30 mm. Thus, the mean July temperature criteria (> 7.8 C) for predicting salmonid abundance and stable stream populations reported by Harig and Fausch (2002) may be further refined when sufficient temperature data are available to calculate degree-days during the growing season. The results of these studies indicate that the "5-8ºC by early July" criteria (USFWS 1998) for selecting candidate habitats for greenback cutthroat trout recovery may be adequate when applied to streams that are not otherwise limited by poor physical habitat conditions. One caveat is that temperatures vary along stream segments due to the influence of groundwater, spring seeps, shading, natural and human-made impoundments, and tributaries that can serve to either warm or cool the stream. This spatial variation in temperature requires more detailed investigation to determine the extent of thermally suitable habitat if thermal suitability criteria are to be applied with the greatest certainty.

It is important to note that the thermal criteria above are derived from studies of predominantly stream resident populations. Greenback cutthroat trout populations in lakes or ponds with inlet or outlet streams that are otherwise too cold to sustain them may nonetheless be stable and reproducing due to the thermal and velocity refugia available in these lakes or ponds. Further research on lake populations should be conducted to further refine our understanding of greenback cutthroat trout physical habitat requirements in a greater variety of physical habitat types.

Despite the apparent limitation of greenback cutthroat trout recruitment by cold temperatures, there is some evidence for cold-temperature adaptation in at least one greenback cutthroat trout population in the Little South Fork of the Cache la Poudre River. Eggs from this population required only 256 degree-days to hatch compared to those from a greenback cutthroat trout population in the Arkansas River Basin. The Arkansas River Basin population required 312 degree-days, a value more typical for trout species in general (Dwyer and Rosenlund 1988).

Spawning habitat

No studies have been conducted to identify spawning habitat requirements specific to greenback cutthroat trout, although Scarnecchia and Bergersen (1986) reported that among three streams they studied that contained either greenback or Colorado River cutthroat trout during 1979-1980, more young fish were found by electrofishing in the stream with a greater proportion of fine to coarse gravel substrate (2-15 mm and 15-63 mm particle sizes, respectively). Others have reported that Gila trout (Rinne 1980) and Apache trout (Harper 1978) of sizes similar to the adult trout reported by Scarnecchia and Bergersen (1986) spawn in a range of gravel sizes that overlap the fine and coarse gravel size classes they used.

Recent evidence suggests that at least one greenback cutthroat trout population may successfully spawn in a lake in Rocky Mountain National Park (Bruce Rosenlund and Chris Kennedy, US Fish and Wildlife Service, unpublished data). Brook trout were removed from Loomis Lake (3,110 m) in 1990, and greenback cutthroat trout were stocked in 1992, and the area has been open to catch-and-release fishing since 1993. There is no spawning inlet or outlet habitat, and it is believed that fish are unable to migrate into the lake from downstream due to a barrier at the outlet of the lake. Periodic fish surveys conducted through 2006 indicate that the population is stable and fish have ranged in size from 155-378 mm since stocking. Greenback cutthroat trout have been observed to exhibit spawning behavior on shoals in the lake, and one young-of-year fry was observed near the shore of the lake during 2004. Loomis Lake has no inlet stream, although significant water does trickle into the lake under rocks on the shore of the lake. Further investigations are required to determine the lifespan of fish and the success rate of spawning and recruitment within the lake.

Rearing habitat

Specific habitat requirements or preferences of young-of-year greenback cutthroat trout have not been widely reported in the scientific literature. However, Cummings (1987) indicated that young-of-year greenback cutthroat trout in Hidden Valley Creek occupied microhabitats along the margins of the stream, characterized by low velocities and fine (silt) substrate. Similar habitat associations were described for coastal cutthroat trout fry less than 30 mm long, which are noted to be weak swimmers and are confined to backwaters, isolated pools, or small shallow sheltered depressions with very low water velocity (Moore and Gregory 1988). This was consistent with microhabitat observations made in high-elevation Colorado streams where either greenback or Colorado River cutthroat trout fry were surveyed by Coleman and Fausch (in press b).

In the southern Rocky Mountain region, the volume of these nursery habitats decreases as flows drop during the summer. This may force young-of-year greenback cutthroat trout, which in many streams do not emerge from redds until late in the summer, to occupy higher-velocity positions in the stream that are more energetically demanding (Cummings 1987). Further studies are needed to determine the extent to which recruitment of young-of-year fish depends on the types of rearing habitat previously described (Moore and Gregory 1988; Coleman and Fausch in press b), and develop methods to better describe and quantify rearing habitat.

Invading brook trout may compound the problem of shrinking lateral habitats for rearing of cutthroat trout. Brook trout spawn during fall and their fry emerge well before cutthroat trout,

Young-of-year greenback cutthroat trout in rearing habitat along stream margin.

when rearing habitat volume is greater. Brook trout fry are thus larger and better able to dominate the best of the dwindling rearing habitat in late summer, when greenback cutthroat trout fry emerge. There is some evidence that the negative effects of brook trout on cutthroat trout populations are strongest during early life-history stages, and the interaction between early life stage brook trout and cutthroat trout may explain why brook trout often completely displace or extirpate cutthroat trout populations in headwater streams in the southern Rocky Mountains (Peterson and Fausch 2004).

Water Quality

Like other salmonids, greenback cutthroat trout are sensitive to water quality parameters that can be altered by both natural and anthropogenic processes. In general, salmonids require cold, clean waters and usually do not persist in waters contaminated by thermal or chemical effluents. Of the water quality parameters that may influence the viability of greenback cutthroat trout populations, temperature has been studied most thoroughly and is best understood. Less understood are the effects of chemicals.

Only two laboratory toxicity studies have been published for greenback cutthroat trout. They describe the effects of low (acidic) pH and aluminum (Woodward and others 1991), and five other chemicals commonly found in the environment due to domestic, industrial, or agricultural uses (Sappington and others 2001). These studies show that larval greenback cutthroat trout are more sensitive to low pH and elevated aluminum than eggs and embryos. The

Table 1. The 12, 24, and 96 h LC50 values for five chemicals commonly found in the environment throughout North America due to their domestic, industrial, or agricultural use.

Chemical	LC50 (Concentrations in µg/L)		
	12 h	24 h	96 h
4-Nonylphenol	380.0	300.0	150.0
Carbaryl	8,500	3,600	1,600
Permethrin	1.00	1.00	1.00
Pentachlorophenol (PCP)	10.0	10.0	10.0
Copper Sulphate	30.0	30.0	30.0

threshold pH for greenback cutthroat trout larvae was 5.0 in the absence of aluminum, but 6.0 with aluminum at 50 µg/l.

These threshold levels should be considered harmful, but they may be further modified in natural environments. The chemical form and toxicity of many chemical toxins can be altered through interactions with other chemicals and temperature effects. Further, acid precipitation in alpine habitats may periodically reduce pH below the threshold levels described above. Continued water quality monitoring in high elevation habitats should be an important part of long-range management of greenback cutthroat trout, particularly where mining operations have been conducted in the watershed.

The 12, 24, and 96 h LC50 (concentration at which 50% of fish die) were determined by Sappington et al (2001) for greenback cutthroat trout exposed to five chemicals common in many environments throughout North America (Table 1). These included: 1) 4-Nonylphenol - a suspected estrogenic compound, 2) Carbaryl - a pesticide and cholinesterase inhibitor, 3) Permethrin - a widely used neurotoxic pesticide, 4) Pentachlorophenol (PCP) - a limited use pesticide used in wood preservation, and 5) Copper sulphate - an agricultural chemical also used in some mining, fish culture, and water treatment and alters cell membrane permeability. Although their LC50's were similar to those of rainbow trout in many cases, greenback cutthroat trout were often slightly more sensitive to these substances, particularly with longer test duration.

Although no systematic study of the effects of metals on greenback cutthroat trout has been conducted, circumstantial evidence suggests that high heavy metal concentrations are detrimental to cutthroat trout populations. Greenback cutthroat trout over 25 mm stocked in Bard Creek survive to adulthood and spawn, despite elevated levels of heavy metals from zinc mining activity, but their eggs or larvae do not survive through the fall. Greenback cutthroat trout larvae are probably very sensitive to zinc, as are their surrogate, rainbow trout, and the closely related Colorado River cutthroat trout (Brinkman and Hanson 2004). However, further research is required to determine the threshold LC50 values for zinc and other heavy metal contaminants common in some high-elevation streams in Colorado due to historic mining operations or natural conditions.

LIFE-HISTORY

Migration and movement

Migratory life-histories related to feeding and reproduction are common in salmonids, including many cutthroat trout subspecies. The extent to which greenback cutthroat trout life-histories were historically migratory is unknown, although Jordan (1891) noted that greenback cutthroat trout moved into irrigation ditches at times, and today some introduced populations in Rocky Mountain National Park migrate short to moderate distances from lakes or ponds into inlet and outlet streams to spawn. Upstream migrations for spawning by stream resident populations are also apparent, although no studies have been conducted to describe such migrations. The migratory potential of most greenback cutthroat populations is limited by the small headwater stream segments they now occupy.

Spawning and Reproduction

Greenback cutthroat trout spawn in the spring or early summer. Although the environmental cues that trigger spawning behavior have not been thoroughly investigated, field observations suggest that fish begin spawning once daily temperatures pass a threshold. Based on many years of field observations and temperature monitoring in Rocky Mountain National Park, the temperature threshold for spawning of greenback cutthroat trout appears to be around 5-8ºC in various waters (USFWS 1998; Bruce Rosenlund and Chris Kennedy, unpublished data). Further, Bulkley (1959) reported that greenback cutthroat trout spawned from July 1-15, 1958, when approximate median water temperatures were 5-7ºC in the headwaters of the Big Thompson River (3,200 m elevation). The exact time of spawning varies with elevation and temperature, such that greenback cutthroat trout in Lytle Pond on Fort Carson (1,889 m) were in spawning condition by early April, whereas those in Upper Hutcheson Lake (3,402 m) have been observed to spawn in mid-July.

Sexual maturity and fecundity are more closely related to size more than age in salmonids. Female greenback cutthroat trout appear to reach sexual maturity after their third or fourth summer and at a length of approximately 180 mm (USFWS 1998). Quinlan (1980) reported that sexual maturity was reached at 146 mm in a population of the closely-related Colorado River cutthroat trout from a cold southern Wyoming stream. The age at which greenback cutthroat trout reach sizes at which they become sexually mature depends on the productivity and temperature of the water they occupy. Nelson (1972) reported that slightly hybridized (Type B) female greenback cutthroat trout from Island Lake, averaging 270 mm long, produced an average of 299 eggs per fish, and Colorado River Cutthroat trout from Trappers Lake, Colorado that averaged 290 mm, averaged 667 eggs (Snyder and Tanner 1960). Dwyer (1981) reported that pure 2-year-old greenback cutthroat trout females from Como Creek (Type A) produced 1.5 eggs per gram of female weight, while 3-year-old females produced 1.4 eggs per gram of female weight. However, the fecundity of hybridized greenback stock may be reduced relative to their genetically pure parental stocks, so the true length-fecundity relationships of genetically pure greenback cutthroat trout and factors which might cause this relationship to vary among populations warrants further investigation.

When spawning, female salmonids dig redds or depressions in the gravel bed of streams, where they deposit eggs as males swim along side and release milt to fertilize them. A female may dig a succession of redds and spawn with more than one male during spawning, depositing a portion of her eggs in each redd. The fertilized eggs, or embryos, remain in the spaces between gravel particles in the redd, where they develop and hatch. After hatching, the sacfry, or alevin, remain predominantly in the gravel until they have consumed most of their yolk. When they emerge from the gravel, fry develop the ability to regulate their buoyancy and move up and down in the water freely, although their poorly developed swimming skills leave them at the mercy of the current unless they find microhabitats sheltered from the current where they can feed on tiny invertebrates and grow.

If fry emerge well before the end of the growing season, they appear to have a good probability of finding sufficient food to grow and store energy to survive their first winter, but field observations and laboratory research suggest that recruitment and total population size in some high-elevation streams are limited in large part by cold summer temperatures and

Spawning greenback cutthroat trout.

short growing seasons (USFWS 1998; Harig and Fausch 2002; Coleman and Fausch in press a, in press b). Salmonids are very vulnerable to mortality due to several physical and biological factors during early life-history stages when limited recruitment of young fish to subadult and adult stages can have major effects on population size and long term viability.

Post-spawning mortality rates in adult greenback cutthroat trout is unknown, but may be high due to the energetic demand of competition among males for access to females, and the investment of energy in egg production and possible spawning migrations. Spawning frequency may be limited in high elevation streams that are poorly productive, particularly of females, due to a more pronounced tradeoff between reproduction and survival. Greenback cutthroat trout may be able to spawn more frequently in warmer, more productive habitats at lower elevation, but few of these populations are available for comparison. Future research stocking in lower elevation habitats may present good opportunities to conduct comparative studies of reproduction, fecundity, and survival over wider range of conditions and help better delineate the features of optimal greenback cutthroat trout habitat.

Size and Growth

The size and growth of greenback cutthroat trout varies with elevation and population size. These differences are likely due to local temperatures throughout the year and competition for resources within larger, denser populations. In general, fish larger than 250 mm are rare in the small, high-elevation streams with short growing seasons where greenback cutthroat trout populations are most commonly found today (Scarnecchia and Bergersen 1986; Young et al 2005). However, greenback cutthroat trout have attained sizes of 356-380 mm in the high-elevation headwaters of the South Fork Cache La Poudre River (2,800 m), where they exceed the size of brook trout in similar habitats (USFWS 1998). Moreover, when 250 mm greenback cutthroat trout from Cascade Creek were transferred to the lower elevation at Lytle Pond (1,889 m), they grew to much larger sizes. One male had reached a length of 510 mm and weight of 2.0 kg in two years. Further studies of tagged greenback cutthroat trout in Lytle Pond indicated a 79 mm and 410 g increase for males, and an 86 mm and 315 g increase for pre-spawning females from April 1991 to April 1992.

Several populations in Rocky Mountain National Park appear to illustrate the effects of population density on growth. Greenback cutthroat trout were stocked in Sandbeach and Pear lakes after nonnative trout were removed. Stocked at 161 mm at a rate of 22.7 – 26.0 kg/ha on June 30, 1989, a sample of these fish had grown an average of 57 mm (range 47-68 mm) after only 10 weeks. A year after stocking, in 1990, fish in both populations had begun to spawn, and growth averaged only 20 mm at Sandbeach Lake from September 1989 to September 1991 (2 years), and only 16 mm at Pear Lake from September 1989 to July 1991 (22 months). Six tagged fish in the large and stable population (118 kg/ha) at Hunters Creek (2,896 m) ranged from 178-252 mm in length, and increased in weight an average of only 6 g, with no change in length, from June 1988 to June 1989. This population is closed to angling, and is thus likely at the maximum density its environment will support.

POPULATION ECOLOGY

Spatial patterns in populations

The Habitat Requirements section described an array of habitats needed to sustain cutthroat trout populations. How the spatial arrangements of these habitats influence greenback cutthroat trout populations has not been fully investigated, but research indicates that it is important in determining population size and persistence probability (Harig and Fausch 2002). Gravels suitable for spawning may have a patchy distribution, and the number of pools suitable as overwintering refugia varies along streams as well. The best foraging habitat may be in the lower, warmer reaches of a stream segment or lakes, whereas the best spawning habitat is in reaches of moderate gradient, well upstream. Some fish may therefore be forced to migrate between spawning, foraging, and overwintering habitats throughout the year, and the relative abundance and spatial distribution of these habitats will therefore limit fish numbers. Recent research on both Colorado River and greenback cutthroat trout populations indicates that individual habitat components are not sufficient to explain abundance, and the authors suggest that larger streams may therefore support much larger populations because they provide a greater diversity of habitat types than smaller streams (Young et al 2005).

Variation in populations over time

Greenback cutthroat trout populations and size structure vary among streams (Young and Guenther-Gloss 2004). Colder, higher-elevation populations closed to angler harvest tend to have relatively few young (small) fish, indicating a greater risk of year class failure, and/or competition with long-lived adults. Populations in these cold streams may therefore be sustained by intermittent recruitment of young fish due to environmental variability or competition from year to year. Conditions in some years may simply be better for recruitment than in others. Conversely, greenback populations in warmer, mid-elevation streams consist of a larger proportion of smaller, younger individuals, reflecting more regular recruitment and a relative rarity of complete year-class failure. Sites included in Young and Guenther-Gloss (2004) are well-established, and at least one (Hunters Creek) was used for egg collections almost every year. Recruitment of young fish in many of these higher elevation populations may also be limited because they are near carrying capacity.

Metapopulations

A metapopulation is a group of geographically distinct populations that are linked by migration of individuals, resulting in gene flow. The amount of migration and gene flow may vary in frequency, timing, and direction between populations, but the persistence of populations is promoted by the migration of individuals among them. Where sufficient connectivity exists among habitats, salmonids are thought to form metapopulations, but the formation of metapopulations in greenback cutthroat trout is currently limited to those that can occur in the portions of stream networks located above migration barriers that prevent nonnative salmonid invasions. Restoration of greenback cutthroat trout populations over larger, connected portions of stream networks should be considered a management goal because of the benefits to persistence of individual populations that are otherwise threatened by local catastrophes (e.g., fire or flash flood), and the maintenance of genetic diversity and adaptability to expected environmental change that could result from migration and gene flow in such a metapopulation. In cases where restoration habitat is restricted to smaller and less complex stream segments, stocking of appropriate genetic stocks may be a successful surrogate to foster genetic exchange assumed to bolster physiological performance and increase long term viability. However, increasing upstream connectivity also increases threats from disease and non-native species.

COMMUNITY ECOLOGY

Historically, the distribution of greenback cutthroat trout extended well downstream into warmer, lower elevation streams (Jordan 1891; Behnke 1992, 2002), and as such they were likely sympatric with several other fishes. Currently, greenback cutthroat trout are often the only fish species present in the isolated headwaters where they remain or have been transferred to preserve and restore populations of the subspecies. The warmer habitats they formerly occupied are now largely dominated by a suite of nonnative fishes. The prevalence of nonnative fish and habitat degradation make it difficult to do more than speculate on the ecology of riverine vertebrate communities throughout the historical range of greenback cutthroat trout and the role of terrestrial and avian predators in these communities. However, studies of greenback cutthroat trout diet and disease have begun to reveal the roles of greenback cutthroat trout as predators in existing aquatic food webs and as hosts to parasites and other disease organisms.

Greenback cutthroat trout as predators

The diet of greenback cutthroat trout is made up mostly of aquatic and terrestrial invertebrates, but studies indicate the relative numbers of each organism consumed may vary, indicating that greenback cutthroat trout are opportunistic feeders that will eat what is available. Bulkley (1959) found that from late June-August 1958, an average of 75% of the stomach contents of greenback cutthroat trout in the headwaters of the Big Thompson Drainage (2,740 – 3,185 m) were terrestrial insects, comprised mostly of hymenoptera (ants, bees, wasps) and diptera (flies). Fausch and Cummings (1986) studied greenback cutthroat trout in Hidden Valley Creek, RMNP (2,690 m), and their data indicated that greenback cutthroat trout are opportunistic feeders that feed on a wide variety of prey organisms. Their diet consisted of a relatively constant proportion of terrestrial invertebrates through September that declined markedly in October, as temperature declined. McGrath (2004) studied the diets of both greenback cutthroat trout and brook trout in streams that contained either one or both of the species (2,837-3,040 m), and found that greenback cutthroat trout consumed more prey overall and a greater variety of prey than brook trout of similar size in most sites where both species were present. As in the other studies, a large proportion of prey consumed was terrestrial invertebrates.

There is little evidence that greenback cutthroat trout consume vertebrate prey, but several observed instances of greenback cutthroat trout predation on vertebrates have been observed that suggest this may be an artifact due to the locales where greenback cutthroat trout have been studied in the field. Whereas Jordan (1891) stated that greenback cutthroat trout were reluctant to accept "flesh" in the Leadville National Fish Hatchery, but readily consumed invertebrates. Fausch and Cummings (1986) further found no young-of-year greenback cutthroat trout in the stomachs of adult greenback cutthroat trout studied in Hidden Valley Creek, although this result may be due in part to more rapid digestion of the soft tissues of young-of-year fish relative to the hard exoskeletons of invertebrates. Further, a 114 mm tiger salamader (*Ambystoma tigrinum*) was found in the stomach of a Cascade Creek greenback cutthroat trout that was illegally taken from Lytle Pond, Fort Carson in 1982, and variation in the Arkansas darter population that shared habitat with greenback cutthroat trout at Lytle Pond also suggested greenback cutthroat trout predation but was not confirmed by stomach analysis. To date, feeding data indicate that greenback cutthroat trout may have a more variable diet than some other salmonids (Behnke 1992, 2002; USFWS 1998), and may explain why they reportedly dominated angler catch, even though they comprised the minority of fish, under catch-and-release regulations (USFWS 1998).

Disease and Parasites

Many bacterial and viral pathogens cause diseases leading to high mortality rates in salmonids in hatcheries, but their occurrence and impact in natural populations of greenback cutthroat trout has not been studied systematically and remains unknown. Several common salmonid diseases and their known causative pathogens include: bacterial coldwater disease (*Flavobacterium psychorophilum*), furunculosis (*Aeromonas salmonicida*), proliferative kidney disease (*Tetracapsula bryosalmonae*), and viral infectious hematopoietic necrosis. Disease testing on body fluids and excreta from Como Creek greenback cutthroat trout collected in 1977, and from Hunters Creek, Upper Hutcheson Lake, and the South Fork Poudre River from 1983-1996, revealed no viral infections in fish from wild populations. One moribund wild fish from Como Creek was infected by bacteria nonobligate to salmonids. However, this fish displayed infestations by several parasites, including *Gyrodactylus* spp., *Glossatella* spp., *Hexamitta* spp., and *Crepidostomumfarionus*.

The parasite of greatest immediate concern to greenback cutthroat trout populations is *Myxobolus cerebralis*, which causes whirling disease in many salmonid species. The parasite is not native to Colorado waters, and was probably introduced and spread through transport, cultivation, stocking, and proliferation of nonnative salmonids. It is particularly noteworthy because research suggests it has the potential to cause near complete mortality during early life-history stages when the parasite attacks the cartilage of juvenile fish, causing abnormal development, deformity, and very high rates of mortality. Near complete failures in recruitment of young age classes of rainbow trout in some Colorado rivers have been attributed to the *M. cerebralis* parasite (Walker and Nehring 1995; Nehring and Walker 1996). Further, after exposure to ambient *M. cerebralis* concentrations in Colorado River water, several cutthroat trout subspecies were as susceptible to whirling disease or more so than rainbow trout (Thompson and others 1999). Although overwinter mortality rates for juvenile greenback cutthroat trout in this study were similar to those of rainbow trout, their mortality rates were the highest of any group in the study when fish were held over for observation during the following summer. This result was consistent with earlier observations that growth and survival rates of greenback cutthroat trout infected with *M. cerebralis* in the lab were markedly lower than those of rainbow trout, despite greenback cutthroat trout showing greater resistence to initial infection by *M. cerebralis* (Markiw 1990, 1992).

The life cycle of the *M. cerebralis* parasite includes four stages. During two of the stages, the parasite is free-living and is transmissible between its two hosts, salmonid fishes and a segmented worm (*Tubifex tubifex*). The favored habitat of *T. tubifex* includes the fine sediments in backwaters of streams and rivers, and those found as substrate in many ponds, lakes, or impoundments. It is probably not mere coincidence that these habitats are also favored by salmonid fry that have recently emerged from their gravel redds, as this places early life-stage salmonids in close proximity to *T. tubifex*, and thus *M. cerebralis*, and may facilitate transmission. The susceptibility of salmonids native to North America to whirling disease is probably due to their evolution in the absence of the parasite, whose natural salmonid host in the Old World appears to be the brown trout, which does not typically develop fatal whirling disease symptoms once infected.

The headwater streams to which greenback cutthroat trout are largely restricted provide less habitat for the *T. tubifex* intermediate host (McAfee 1998), which may lessen both the risk and intensity of *M. cerebralis* infection. Headwater streams in the southern Rocky Mountains are characterized by cold water temperatures, high gradient, and sand/gravel substrates with limited fine materials. Several greenback cutthroat trout populations or downstream surrogates have been tested for *M. cerebralis* and found to be negative. However, Zimmerman Lake in the upper Poudre River drainage, the designated feral brood lake for the South Platte greenback cutthroat trout, was found to be positive for *M. cerebralis*.

As myxospores, *M. cerebralis* can survive harsh conditions for long periods of time, and it is believed that the spores can be spread among streams on contaminated clothing or wading equipment if such gear is not cleaned or dried adequately between uses. Habitat degradation due to land use and grazing practices can introduce fine sediments and create additional habitat where *T. tubifex* can proliferate and serve as local sources of the *M. cerebralis* parasite. In addition, salmonids are very mobile and as adults can easily carry whirling disease upstream to the migration barriers that protect native cutthroat trout populations. Therefore, although many headwater greenback cutthroat trout populations are remote, and are subjected to minimal angling and limited habitat degradation, they should not be considered invulnerable to whirling disease. The upstream migration barriers that protect these populations can fail, or infected fish can be intentionally caught and released upstream. Very little would be required to inadvertently introduce *M. cerebralis* into many conservation populations.

RESEARCH NEEDS

There are still important gaps in our knowledge of the life-history and ecology of the greenback cutthroat trout. Fisheries Biologists should consider to pursue research to fill these gaps to help insure that future conservation and management efforts grow increasingly effective. In addition to the need for further research identified in the previous sections, there is also a need to study the effects of isolation management on greenback cutthroat trout populations. While isolating populations above upstream migration barriers has helped preserve the subspecies, by protecting populations from invasions by nonnative salmonids and the introduction of parasites and disease, some isolated habitats are relatively small and there is a potential for deleterious effects from inbreeding. Indeed, deformities seen in some fish collected from Como Creek (Chris Kennedy, unpublished data) may be an example of inbreeding effects. As biologists gather more information on the population genetics, life-history, and ecology of greenback cutthroat trout, management activities should be adjusted when feasible to reflect new knowledge and insure that conservation goals are met with the greatest possible efficiency.

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