Chapter 2

Colorado River Cutthroat Trout

Michael K. Young,
USDA Forest Service, Rocky Mountain Forest and Range Experiment Station,
222 S. 22nd Street, Laramie, Wyoming 82070

Introduction

The Colorado River cutthroat trout historically occupied portions of the Colorado River drainage in Wyoming, Colorado, Utah, Arizona, and New Mexico (Behnke 1992). Though it is now restricted to headwater streams and lakes, its original distribution probably included portions of larger streams, such as the Green (Simon 1935), Yampa, White, Colorado, and San Juan rivers.

Behnke and Zarn (1976) speculated that this subspecies was absent from the lower reaches of many large rivers because of thermal barriers in summer. Yet other subspecies of cutthroat trout have seasonally migrated over 100 km, usually upstream in spring and downstream in autumn (Bjornn and Mallet 1964). Similarly, in late fall brown trout have moved over 35 km to habitats considered marginal in summer (Meyers et al. 1992). Thus portions of these lower reaches may have become acceptable in winter as water temperatures moderated and may partially explain the apparently disjunct historical distribution of this subspecies.

Life History Characteristics

The diversity of life histories exhibited by this subspecies has probably been reduced. Adfluvial stocks may have occupied a number of high-elevation lakes (e.g., on the southwestern slope of the Wind River Range in Wyoming [Simon 1935] or on the west slope of the Park Range in Colorado), but these stocks have been largely eliminated. Most remaining populations are fluvial or resident, though reestablished lacustrine stocks of Colorado River cutthroat trout have been reported in Wyoming (R. Remmick, Wyoming Game and Fish Department, pers. commun.) and Rocky Mountain National Park in Colorado.

Spawning by this subspecies begins after flows have peaked in spring or early summer and ends before runoff subsides (Quinlan 1980; Young, pers. obs.). Water temperature may also act as a cue for the timing of spawning (Quinlan 1980). In tributaries of the North Fork Little Snake River, Wyoming, adults returned to the mainstem shortly after spawning (Young, unpubl. data). In contrast, many spawning fish remained in tributaries of Trappers Lake, Colorado, after late July (Snyder and Tanner 1960). Fluvial Colorado River cutthroat trout have spawned in intermittent streams that were unsuitable adult habitat (Jespersen 1981; cf. Erman and Hawthorne 1976). In Trappers Lake, 16% of the spawning run consisted of repeat spawners, and most had spawned the previous year (Snyder and Tanner 1960), but the proportion and frequency of repeat spawning in fluvial or resident populations is unknown.

The fecundity of Colorado River cutthroat trout presumably varies with length, location, and life history. Based on 13 trout from 149 to 210 mm from Solomon Creek, Wyoming, Quinlan (1980) related total length in mm (x) to egg number (y) by using the equation $y = -266.56 + 2.63(x)$. Fecundity of 16 females (mean length 290 mm) from a tributary to Trappers Lake was 667 eggs (Snyder and Tanner 1960).

Water temperature, influenced by elevation and annual climatic variation, controls the time of emergence, which tends to be in late summer in streams still containing this subspecies. Near 2,700 m above mean sea level in Wyoming, Jespersen (1981) first found swim-up fry in late August, but also found alevins in the substrate as late as early September. At 2,708 m above mean sea level in Colorado, Scarnecchia and Bergersen (1986) observed emerging fry in late July and early August, as did Snyder and Tanner (1960) and Drummond (1966) in tributaries of

Trappers Lake near 2,950 m above mean sea level. In these tributaries, most fry began migrating to the lake shortly after emergence, and migration continued through mid-September, though some fry were thought to remain in the tributaries over winter (Snyder and Tanner 1960).

Length and age at maturity are related to food abundance and the length of the growing season. Colorado River cutthroat trout reached maturity at age 3 and averaged 146 mm in the North Fork Little Snake River drainage; no fish were older than age 6 (as aged by scales), and few were over 200 mm (Quinlan 1980). In the same watershed, Jespersen (1981) found no fish larger than 250 mm, and he estimated abundances from 77 to 609 fish/km and biomasses from 3.1 to 109.4 kg/ha. Growth rates in this stream were one-third to one-half those reported for cutthroat trout elsewhere in the western United States (Bozek et al. 1994). Similarly, the largest Colorado River cutthroat trout observed in Little Green Creek, Colorado, was 202 mm (Scarnecchia and Bergersen 1986). They also noted that production and the production:biomass ratio of Colorado River cutthroat trout were among the lowest reported for salmonids, which they attributed to the short growing season at high elevations.

Nevertheless, this subspecies can reach larger sizes. Fish less than 200 mm (from the North Fork Little Snake River drainage) were transplanted to a lower-elevation pond and reached 380 mm after 2 years (M. Fowden, Wyoming Game and Fish Department, pers. commun.). Remmick (no date) reported that this subspecies commonly exceeded 254 mm and reached 335 mm in tributaries of the Green River, Wyoming, especially those streams with beaver ponds. In contrast, lake-dwelling Colorado River cutthroat trout averaged 325 mm at age 3 (Drummond 1966), and older fish occasionally surpassed 470 mm (Colborn 1966). Behnke (1992) cited unconfirmed historical accounts of this subspecies reaching 10 kg west of the Continental Divide in Colorado.

Habitat Relations

The seasonal habitat requirements of various life stages of Colorado River cutthroat trout have rarely been studied, and then largely in summer. For example, Binns (1977) provides information on water quality and habitat from 13 streams in Wyoming, but conclusions were based on a single visit to each stream between July and October from 1968 to 1975.

Typical of most Salmoninae, Colorado River cutthroat trout spawn in substrate predominantly composed of gravel. The mean dominant particle size in 34 redds in the North Fork Little Snake River drainage was 30 mm (Jespersen and Conder 1986). The geometric mean particle size of 41 redds in the North Fork Little Snake River drainage averaged 10.4 mm and ranged from 3.7 to 22.8 mm (Young 1989). Laboratory studies revealed that geometric mean particle sizes from 13.8 to 15.9 or larger yielded the best survival (Young et al. 1991).

Redds tend to be located where velocity, depth, and bottom configuration induce water flow through the stream substrate (Young 1989). Jespersen and Conder (1986) measured a mean depth of 18 cm and a mean nose velocity of 34 cm/s over 34 recently constructed redds in the North Fork Little Snake River watershed. By late summer, flows had declined substantially in the spawning area; 21% of the redds were dry, but fry may have already emerged. Near the time that eggs hatched in 1987, Young (unpubl. data) measured a mean depth of 11 cm and a mean nose velocity of 15 cm/s over 33 redds in that watershed.

Bozek and Rahel (1991a) characterized fry summer microhabitats as sites with water velocities slower than 6 cm/s and in water deeper than 3 cm; woody debris, boulders, and rootwads sheltered these sites from higher water velocities. Yet many reaches with suitable microhabitats contained no fry, and they concluded that the presence of spawning gravel (and thus redds) was requisite for the presence of fry.

The identification of variables important to adults has been inconsistent. Some researchers have electrofished stream reaches (Jespersen 1981) or individual habitat types (Herger 1993) to relate fish abundance to habitat characteristics. A multiple regression equation including spawning habitat, cover, and riffle water velocity as independent variables accounted for 78% of the variation in Colorado River cutthroat trout biomass in the North Fork Little Snake River drainage, and spawning habitat was the single most important variable (Jespersen 1981). Herger (1993) found that most Colorado River cutthroat trout larger than 152 mm were in pools, and that pool depth influenced trout density. Yet cover features were not related to trout abundance, nor was the kind of pool, e.g., plunge pool or dammed pool. Also, the density of fish in pools increased as the flows declined over the summer (Herger 1993).

The repeated location of individual fish with radiotelemetry has yielded different results. Young (unpubl. data) compared the characteristics of habitats used by and available to adult Colorado River cutthroat trout in the North Fork Little Snake River drainage. Nearly 40% of the habitats occupied by these fish were created by coarse woody debris, yet fewer than 10% of the stream consisted of such sites. Habitats created by meanders were significantly underused. The mean depth of used habitats was significantly greater than that of available sites. Used sites had significantly lower average water velocities near the stream bottom and surface than those available. But there were no significant differences in mean water velocity or in distance to cover between used and available habitats, and fish positions tended to be significantly farther from the banks than would be expected by chance alone.

Low fish densities may further confound interpretations of habitat use. Herger (1993) reported that many apparently suitable pools in the North Fork Little Snake River drainage contained no fish. Quinlan (1980) noted that large pools in the same drainage typically contained one adult Colorado River cutthroat trout and few or no juveniles.

Additionally, fish movement complicates the assessment of habitat use, and the delineation of populations. Research on several cutthroat trout subspecies has suggested that most small-stream inhabitants are residents with short home ranges (e.g., 18 m, Miller 1957; 4 m, Heggenes et al. 1991), but this may have resulted from methodological constraints (Gowan et al., in press). Quinlan (1980) suggested that Colorado River cutthroat trout did not migrate in the North Fork Little Snake River drainage. But Jespersen (1981) noted that stream reaches in different portions of the North Fork Little Snake River watershed contained different age structures of Colorado River cutthroat trout (i.e., smaller fish upstream, larger fish downstream), and Remmick (no date) observed this pattern in tributaries and the main stem of Rock Creek, Wyoming; both considered this evidence of fish movement. Also, Jespersen (1981) captured some juvenile fish that were migrating downstream in late summer and early fall. Young (unpubl. data) found that adult Colorado River cutthroat trout in the North Fork Little Snake River drainage occupied home ranges over 1,000 m from June to mid-August. After spawning and leaving tributaries, adults moved both up- and downstream from tributary mouths. Minimum weekly movement in late June and early July averaged 125 m, but declined to 14 m by mid-August.

Identifying distinct populations may be difficult if fish move to different streams. For example, a single radio-tagged adult occupied Green Timber Creek, Harrison Creek, and the North Fork Little Snake River above and below the mouths of these tributaries within 3 weeks (Young, unpubl. data). Snyder and Tanner (1960) reported that several males marked in one tributary to Trappers Lake were recaptured 4 weeks later in another tributary at the opposite end of the lake. Traditionally, different tributaries were believed to contain discrete populations, but the mobility of fishes makes this view questionable (Fausch and Young, in press). The characteristics of natural barriers to movement that might isolate populations have not been studied, but Snyder and Tanner (1960) suggested that a 100-m reach with a 19.3% gradient blocked spawning migrations, whereas a 17.3% gradient did not.

Biotic Interactions

Colorado River cutthroat trout evolved in sympatry with several other species, but no closely related salmonids. In the Wyoming portion of the North Fork Little Snake River watershed, Colorado River cutthroat trout are sympatric only with mottled sculpin, though they historically shared nearby reaches with flannelmouth sucker, bluehead sucker, mountain sucker, speckled dace, roundtail chub, mountain whitefish (Eiserman 1958), and probably Colorado squawfish (Baxter and Simon 1970). Other portions of the historical range of Colorado River cutthroat trout also contained species of sculpins (Cottidae), suckers (Catostomidae), and minnows (Cyprinidae). The past or current influence of these other species on Colorado River cutthroat trout is unknown. Only anecdotal evidence exists on the influence of other vertebrates, such as predatory birds and mammals or beaver, on this subspecies. For example, dippers (*Cinclus mexicanus*) captured young-of-the-year trout from stream margins in the North Fork Little Snake River (M. Bozek, National Biological Survey, pers. commun.), and mink (*Mustela vison*) preyed on adults in this watershed in late autumn (S. Pearce, Rocky Mountain Forest and Range Experiment Station, pers. commun.).

The diets of Colorado River cutthroat trout have not been comprehensively studied. Colborn (1966) noted that amphipods, other plankton, dipterans, and terrestrial hymenopterans were important components of the summer diet of Colorado River cutthroat trout in Trappers Lake, Colorado. Small fish were present but rarely eaten. In contrast, adult fish in a tributary to Trappers Lake contained an average of 61 fry (Snyder and Tanner 1960). Bozek et al. (1994) failed to find any young-of-the-year in stomach samples from larger Colorado River cutthroat trout in the North Fork Little Snake River. In streams of the upper Green River drainage, Colorado River cutthroat trout primarily ate dipterans and ephemeropterans, but also consumed most of the available invertebrates (Remmick, no date). In Harrison Creek, Wyoming, a one-day sample revealed that adult Colorado River cutthroat trout ate more large food items and a greater proportion of terrestrial insects than did smaller fish (Bozek et al. 1994). Dipterans constituted the dominant food of all size classes.

The behavior patterns of this subspecies may reveal the relative importance of foraging compared with predator avoidance. Most young-of-the-year trout of this subspecies were visible to observers, and nearly half these fish refused to escape to cover despite disturbance (Bozek and Rahel 1991b). Young (unpubl. data) found that Colorado River cutthroat trout could be seen 75% of the time during the day after being located by radiotelemetry. In contrast, brown trout in nearby streams were only visible 10% of the time once located (Young, unpubl. data). Furthermore, brown trout activity peaked near midnight, whereas the activity of Colorado River cutthroat trout declined at night, but peaked at various times during the day. Moreover, coastal cutthroat trout may choose microhabitats based on food availability rather than on the presence of cover (Wilzbach 1985), possibly because foraging efficiency is influenced by light intensity (Schutz and Northcote 1972; Wilzbach et al. 1986), and this behavior may also apply to Colorado River cutthroat trout. Because their daytime positions are not associated with banks or overhead cover, Colorado River cutthroat trout may be risking greater predation to focus on daytime foraging.

Very little is known about the diseases and parasites of this subspecies. In the North Fork Little Snake River drainage, *Gyrodactylus* is present and may cause death of severely stressed fish (Jespersen 1981). Other data are not available.

Reasons for Concern

The abundance and distribution of Colorado River cutthroat trout have declined so much since the arrival of Europeans that calls have been made for federal listing (Behnke and Zarn 1976). Behnke (1979) stated that the Colorado River cutthroat trout occupied less than 1% of its historical range. Martinez (1988) reported that of 37 populations in northwestern Colorado sampled from 1978 to 1987, 12 apparently declined in genetic purity, 3 were replaced by populations of brook trout, and 1 population disappeared, possibly because of overharvest. By 1977, Colorado River cutthroat trout in Wyoming were thought to be restricted to 40 streams and 2 lakes, and only 8 of these populations were regarded as genetically pure, based on meristic analyses (Binns 1977). Furthermore, most lotic populations were in isolated, headwater streams with average daily flows less than 0.85 m^3/s and often less than 0.14 m^3/s. Stream gradients usually exceeded 4%, and all fish were found above 2,290 m. Based on samples from 17 Wyoming streams, Oberholtzer (1990) estimated that there were 52 adult Colorado River cutthroat trout per km of stream.

Other concerns include the loss of novel stocks and the fragmentation of habitats. Most adfluvial stocks have been lost, though some are being reestablished in lakes in Rocky Mountain National Park from a population stocked in the Williamson lakes, California, in 1931 (Pister 1990). Most streams in the North Fork Little Snake River watershed that contain Colorado River cutthroat trout have been fragmented by the installation of water diversion structures that limit up- and downstream fish passage (Oberholtzer 1990). Streams in other watersheds often have populations of nonnative salmonids in lower reaches that seemingly prevent recolonization by Colorado River cutthroat trout.

Causes of the Decline

Introductions of nonnative salmonids may have had the greatest effect on Colorado River cutthroat trout. Stocking of these nonnative salmonids has been widespread since before 1900, and records of many introductions do not exist. More recent records for the North Fork Little Snake River drainage suggest that rainbow trout were first introduced in 1950 and Yellowstone cutthroat trout and brook trout in 1936 (Oberholtzer 1987). In the Savery Creek drainage, tributary to the Little Snake River, rainbow, brook, and brown trout were first introduced in 1936 and fine-spotted or Yellowstone cutthroat trout possibly were introduced in 1933 (Eiserman 1958). Rainbow trout were first stocked in 1915 in the Smiths Fork, an eventual tributary to the Green River in Wyoming (M. Fowden, Wyoming Game and Fish Department, pers. commun.). Rainbow, brook, brown, golden, and lake trout and coho salmon were introduced into the northern and eastern portions of the Green River drainage before 1934 (Simon 1935). Culture and distribution of nonnative salmonids began in Colorado in 1872 (Wiltzius 1985). Trappers Lake, historically the major source of Colorado River cutthroat trout for stocking throughout Colorado, was planted with Yellowstone cutthroat trout from 1943 to 1950 (Snyder and Tanner 1960).

Nonnative salmonids affect populations of Colorado River cutthroat trout in different ways. Brook trout usually oust most subspecies of inland cutthroat trout when in sympatry, especially at lower elevations and in low-gradient streams (Fausch 1989; M. Fowden, Wyoming Game and Fish Department, pers. obs.). In one portion of Douglas Creek, Wyoming, brook trout effectively replaced Colorado River cutthroat trout between 1982 and 1986 (Oberholtzer 1990). Apparently following a single 1950 planting in a headwater lake, brook trout replaced Colorado River cutthroat trout in the lake and in tributaries throughout the Battle Creek, Wyoming, drainage (Eiserman 1958). Brook trout also supplanted Colorado River cutthroat trout in the headwater tributary of the Colorado River between 1970 and 1975 (Behnke and Zarn 1976). Competition is often suspected as the mechanism leading to replacement, but this has not been demonstrated (Fausch 1988; Griffith 1988). Nevertheless, water temperature can affect the outcome of competitive interactions between these species (DeStaso and Rahel 1994), and this may confer a competitive advantage to brook trout at lower elevations.

Rainbow trout and nonnative subspecies of cutthroat trout readily hybridize with Colorado River cutthroat trout and produce fertile offspring. By 1959, nearly one-third of the spawning run in Trappers Lake consisted of Yellowstone cutthroat trout and occasionally rainbow trout (Snyder and Tanner 1960), which led to the development of a hybrid swarm (Martinez 1988). Also, two previously pure populations in Colorado River tributaries appeared contaminated by rainbow trout genes (Martinez 1988). At least initially, more populations of Colorado River cutthroat trout may have been lost through hybridization than through any other cause (Behnke and Zarn 1976).

A wide variety of land management practices have been suggested to affect populations of Colorado River cutthroat trout. Binns (1977) considered many foothill streams in Wyoming that contained this subspecies to be degraded by overgrazing. Elevated concentrations of lead (Quinlan 1980) and copper (Jespersen 1981) have been found in the North Fork Little Snake River drainage and may be limiting fish abundance. Haggerty Creek, Wyoming, contains toxic effluents from an abandoned copper mine that have eliminated nearly all fish downstream (Oberholtzer 1987). Ironically, this contamination has isolated populations of Colorado River cutthroat trout in several tributaries of Haggerty Creek and protected them from invasion by brook trout and rainbow trout. Water diversion has reduced flows throughout much of the North Fork Little Snake River watershed. Jespersen (1981) concluded that the abundance of Colorado River cutthroat trout in the North Fork Little Snake River and a tributary, Green Timber Creek, would increase from 42 to 142% if adequate instream flows were returned to each stream. These diversions also have fragmented streams, restricting movement between formerly connected populations and creating small, isolated populations that may be more liable to go extinct.

Even when the effects of land management are discernable, the consequences for fish may be unknown. For example, a sediment spill in Green Timber Creek in May 1988 was presumed to harm Colorado River cutthroat trout. Whereas mean fish counts increased 73% after the spill, mean fish size declined 25%. The abundance of spawning gravel, and thus juvenile fish, seems to have increased, but deeper pools occupied by adults may have been filled in by sediment and reduced the abundance of this age class.

Though this subspecies has been regarded as the "canary in the mine" with regard to habitat degradation (Behnke and Benson 1980), it has also persevered in suboptimal habitats. Binns (1977) noted that Colorado River cutthroat trout sometimes persisted in marginal, degraded habitats, often as the only fish species. Behnke and Zarn (1976) also reported that Colorado River cutthroat trout remained in such habitats despite introductions of rainbow trout, and they considered these populations worthy of preservation for this ability.

Unrestricted angling may also pose a threat to populations of this subspecies. Quinlan (1980) reported capturing 50 Colorado River cutthroat trout in 4 to 6 hours, and four individuals caught 48 trout in 4 hours from the West Branch of the North Fork Little Snake River (Eiserman 1958). In one year, anglers apparently removed at least one-third of the adult Colorado River cutthroat trout from Ted Creek, Wyoming, and this loss appeared to change the age structure in the stream the following year. Remmick (no date) considered increased fisherman access detrimental to populations of this subspecies.

Current Management

The decline in abundance of this subspecies has been acknowledged by several agencies. Colorado River cutthroat trout are classified as a Category 2 species by the USDI Fish and Wildlife Service and a sensitive species by Regions 2 and 4 of the USDA Forest Service, and designated with special status in Colorado, Utah, and Wyoming. Now, management plans for this subspecies are complete for northwestern Colorado and south-central Wyoming and drafted for west-central Colorado and all of Utah.

Management of this subspecies has taken several forms. Surveys of the distribution of this subspecies have been completed in south-central Wyoming (Oberholtzer 1990), west-central Wyoming (Remmick, no date), and northwestern Colorado (Martinez 1988; D. Vos, White River National Forest, pers. commun.), but undiscovered populations probably remain. In Wyoming, many populations are protected by fishing closures or catch-and-release regulations. In some waters containing this subspecies, Colorado has prohibited harvest and only allows the use of artificial flies and lures. In contrast, Utah has chosen not to apply special regulations to streams containing this subspecies to avoid attracting public attention (Utah Division of Wildlife Resources, unpubl. document). Certain streams thought to contain genetically pure Colorado River cutthroat trout have been artificially barricaded to prevent the invasion of nonnative fishes. Other streams have received human-made structures designed to increase habitat quantity and quality, or are undergoing changes in land management to improve stream habitat. Finally, a few populations have been evaluated by electrophoresis (Leary 1990; Leary et al. 1993) or mtDNA analysis (Shiozawa et al. 1993) to determine their genetic integrity, but most population evaluations have been based only on visual assessments of morphology and meristics (Binns 1977).

Research Needs

Our understanding of this subspecies is minimal. Basic biological information, such as age at maturity, fecundity, life span, proportion of repeat spawners, spawning frequency, age structure, or even density is lacking for most populations. Furthermore, the timing and magnitude of seasonal movements of most populations and the environmental factors controlling population abundance and structure are unknown. Consequently, we must address such simple biological questions and complex long-term and large-scale problems as: (1) How does the life history of the remaining populations vary? How is this variation affected by land and species management? (2) Do populations seasonally shift their habitat use and position in a watershed? Have we fragmented populations by restricting access to portions of watersheds? Can we calculate the risk of extinction of these populations? Alternatively, if we reconnect streams, how fast will these populations expand into the newly available habitat? Does or can this subspecies form metapopulations? (3) What environmental factors affect the abundance of this subspecies, and how do these effects vary seasonally and by fish life stage? and (4) Historically, how have populations responded to natural disturbances and the ensuing vegetative succession, i.e., what successional sere supports the greatest population density, or what combination of seres are necessary to maintain habitats for all life stages?

Literature Cited

Baxter, G.T., and J.R. Simon. 1970. Wyoming fishes. Wyoming Game and Fish Department, Cheyenne. Bulletin 4.

Behnke, R.J. 1979. Monograph of the native trouts of the genus *Salmo* of western North America. USDA Forest Service, Rocky Mountain Region, Denver, Colorado.

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

Behnke, R.J., and D.E. Benson. 1980. Endangered and threatened fishes of the upper Colorado River basin. Cooperative Extension Service, Colorado State University, Fort Collins. Bulletin 503A.

Behnke, R.J., and M. Zarn. 1976. Biology and management of threatened and endangered western trouts. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. General Technical Report RM–28.

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

Bjornn, T.C., and J. Mallet. 1964. Movements of planted and wild trout in an Idaho river system. Transactions of the American Fisheries Society 93:70–76.

Bozek, M.A., L.D. DeBrey, and J.A. Lockwood. 1994. Diet overlap among size classes of Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in a high-elevation mountain stream. Hydrobiologia 273:9–17.

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

Bozek, M.A., and F.J. Rahel. 1991b. Comparison of streamside visual counts to electrofishing estimates of Colorado River cutthroat trout fry and adults. North American Journal of Fisheries Management 11:38–42.

Colborn, L.G. 1966. The limnology and cutthroat trout fishery of Trappers Lake, Colorado. Department of Game, Fish, and Parks, Denver, Colorado. Fisheries Research Division Special Report 9.

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

Drummond, R.A. 1966. Reproduction and harvest of cutthroat trout at Trappers Lake, Colorado. Department of Game, Fish, and Parks, Denver, Colorado. Fisheries Research Division Special Report 10.

Eiserman, F. 1958. A fisheries survey of the Little Snake River drainage. Wyoming Game and Fish Commission, Cheyenne. Fisheries Technical Report 6.

Erman, D.C., and V.M. Hawthorne. 1976. The quantitative importance of an intermittent stream in the spawning of rainbow trout. Transactions of the American Fisheries Society 6:675–681.

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

Fausch, K.D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook charr (*Salvelinus fontinalis*) and other resident salmonids in streams? Physiology and Ecology Japan, Special Volume 1:303–322.

Fausch, K.D., and M.K. Young. In press. Movement of resident stream fishes and evolutionarily significant units: a cautionary tale. *In* J.L. Nielsen, ed. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Bethesda, Maryland.

Gowan, C., M.K. Young, K.D. Fausch, and S.C. Riley. In press. Restricted movement in stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences.

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

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

Herger, L.G. 1993. Assessment of the basin-wide habitat inventory technique relative to Colorado River cutthroat trout. Master's thesis, University of Wyoming, Laramie.

Jespersen, D.M. 1981. A study of the effects of water diversion on the Colorado River cutthroat trout (*Salmo clarki pleuriticus*) in the drainage of the North Fork of the Little Snake River in Wyoming. Master's thesis, University of Wyoming, Laramie.

Jespersen, D.M., and A. Conder. 1986. Colorado River cutthroat trout spawning and incubation habitat summary. Wyoming Game and Fish Department, Cheyenne. Administrative Report.

Leary, R.F. 1990. Genetic and meristic analysis of Colorado River cutthroat trout. Division of Biological Sciences, University of Montana, Missoula. Population Genetics Laboratory Report 90/2.

Leary, R.F., G.K. Sage, and F.W. Allendorf. 1993. Genetic variation in Colorado River cutthroat trout in the North Fork Little Snake River drainage, Wyoming. Division of Biological Sciences, University of Montana, Missoula. Wild Trout and Salmon Genetics Laboratory Report 93/3.

Martinez, A.M. 1988. Identification and status of Colorado River cutthroat trout in Colorado. American Fisheries Society Symposium 4:81–89.

Meyers, L.S., T.F. Thuemler, and G.W. Kornely. 1992. Seasonal movements of brown trout in northeast Wisconsin. North American Journal of Fisheries Management 12:433–441.

Miller, R.B. 1957. Permanence and size of home territory in stream-dwelling cutthroat trout. Journal of the Fisheries Research Board of Canada 14:687–691.

Oberholtzer, M. 1987. A fisheries survey of the Little Snake River drainage, Carbon County, Wyoming.

Fish Division, Wyoming Game and Fish Department, Cheyenne. Project 5086–01–8501.

Oberholtzer, M. 1990. Current status of Colorado River cutthroat trout in the Little Snake River enclave. Fish Division, Wyoming Game and Fish Department, Cheyenne. Project 5090–28–8501.

Pister, P. 1990. Pure Colorado trout saved by California. Outdoor California 51:12–15.

Quinlan, R.E. 1980. A study of the biology of the Colorado River cutthroat trout (*Salmo clarki pleuriticus*) population in the North Fork of the Little Snake River drainage in Wyoming. Master's thesis, University of Wyoming, Laramie.

Remmick, R. No date. A survey of native cutthroat populations and associated stream habitats in the Bridger-Teton National Forest. Fish Division, Wyoming Game and Fish Department, Cheyenne.

Scarnecchia, D.L., and E.P. Bergersen. 1986. Production and habitat of threatened greenback and Colorado River cutthroat trouts in Rocky Mountain headwater streams. Transactions of the American Fisheries Society 115:382–391.

Schutz, D.C., and T.G. Northcote. 1972. An experimental study of feeding behavior and interaction of coastal cutthroat trout (*Salmo clarki*) and Dolly Varden (*Salvelinus malma*). Journal of the Fisheries Research Board of Canada 29:555–565.

Shiozawa, D.K., R.P. Evans, and R.N. Williams. 1993. Relationships between cutthroat trout populations from ten Utah streams in the Colorado River and Bonneville drainages. Utah Division of Wildlife Resources, Ogden. Interim Report. Contract 92-2377.

Simon, J.R. 1935. A survey of the waters of the Wyoming National Forest. U.S. Department of Commerce, Bureau of Fisheries, Washington, D.C.

Snyder, G.R., and H.A. Tanner. 1960. Cutthroat trout reproduction in the inlets to Trappers Lake. Colorado Department of Game and Fish, Denver. Technical Bulletin 7.

Wiltzius, W.J. 1985. Fish culture and stocking in Colorado, 1872–1978. Colorado Division of Wildlife, Fort Collins. Division Report 12.

Wilzbach, M.A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). Canadian Journal of Fisheries and Aquatic Sciences 42:1668–1672.

Wilzbach, M.A., K.W. Cummins, and J.D. Hall. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology 67:898–911.

Young, M.K. 1989. Effect of substrate composition on the survival to emergence of Colorado River cutthroat trout and brown trout. Doctoral dissertation, University of Wyoming, Laramie.

Young, M.K., W.A. Hubert, and T.A. Wesche. 1991. Selection of measures of substrate composition to estimate survival to emergence of salmonids and to detect changes in stream substrates. North American Journal of Fisheries Management 11: 339–346.