Transactions of the American Fisheries Society 136:1381–1392, 2007

DOI: 10.1577/T07-017.1

[Article]

Competition and Predation as Mechanisms for Displacement of Greenback Cutthroat Trout by Brook Trout

C. C. McGrath*[1] and W. M. Lewis Jr.

Department of Ecology and Evolutionary Biology and Center for Limnology, Cooperative Institute for Research in Environmental Sciences, 216 UCB, University of Colorado, Boulder, Colorado 80309-0216, USA

Abstract.—Cutthroat trout *Oncorhynchus clarkii* frequently are displaced by nonnative brook trout *Salvelinus fontinalis*, but the ecological mechanisms of displacement are not understood. Competition for food and predation between greenback cutthroat trout *O. c. stomias* and brook trout were investigated in montane streams of Colorado. A replicated field study was used to describe the population density, diet, stomach fullness, and body condition of the two species in allopatry and sympatry. Population data confirmed that brook trout displaced greenback cutthroat trout at sites where the species occur together. The diets of the two species were different; cutthroat trout consumed more prey items and a wider variety of prey than brook trout. Sympatry did not influence gut fullness or body condition for either species. Predation occurred at low rates that did not account for declines in populations of greenback cutthroat trout. Instead, population data suggest that the displacement of greenback cutthroat trout by brook trout occurs through a bottleneck on recruitment due to the mortality of eggs or juvenile cutthroat trout.

The greenback cutthroat trout *Oncorhynchus clarkii stomias*, which is endemic to the South Platte and Arkansas rivers, is listed as threatened under the U.S. Endangered Species Act. Like many subspecies of cutthroat trout *O. clarkii*, greenback cutthroat trout declined in abundance during the late 1800s and early 1900s because of harvest, habitat alteration, and introduction of nonnative salmonids (Behnke 2002). Only 18 populations are known to have survived. Recovery efforts initiated in the 1970s have focused on identification of suitable habitat, removal of nonnative salmonids from restoration areas by means of antimycin, and stocking of hatchery-reared greenback cutthroat trout to establish self-sustaining populations. Restoration sites typically are headwater streams and lakes that are isolated from nonnative fishes by barriers, such as waterfalls or dams. As of 2005, about 60 such sites contained greenback cutthroat trout, but many of these populations are not considered to be stable because of small population size, lack of reproduction, or the presence of nonnative salmonids (USFWS 1998; Young and Harig 2001; Young et al. 2002).

Efforts to restore greenback cutthroat trout have been hindered by the presence of nonnative salmonids, including rainbow trout *O. mykiss*, Yellowstone cutthroat trout *O. c. bouvieri*, brown trout *Salmo trutta* and, most frequently, brook trout *Salvelinus fontinalis*. Brook trout occur at about 25% of greenback cutthroat trout sites as a result of incomplete eradication, migration upstream past ineffective barriers, or reintroduction by anglers (Trotter 1987; Young 1995; USFWS 1998; Young et al. 2002).

Greenback cutthroat trout and brook trout have similar habitat requirements, and both species are sensitive to habitat disturbance (Behnke 2002). Both species feed on a variety of aquatic and terrestrial invertebrates and may sometimes eat small fish or amphibians (Bulkley 1959; Cummings 1987; Young and Harig 2001). Greenback cutthroat trout spawn in late spring or early summer and fry emerge in August, while brook trout spawn in the fall and fry emerge in early summer. Typically, greenback cutthroat trout spawn at age 3 and older and brook trout at age 2 and older (USFWS 1998; Behnke 2002).

The mechanisms of displacement of native fishes by introduced species include hybridization, disease transmission, competition, and predation. Fall-spawning brook trout do not hybridize with greenback cutthroat trout, although rainbow trout and other cutthroat trout subspecies readily hybridize with greenback cutthroat trout (Allendorf et al. 2001). Disease transmission from brook trout does not account for declines in greenback cutthroat trout (USFWS, unpublished data) or the closely related Colorado River cutthroat trout (*O. c. pleuriticus*; Peterson and Fausch 2002). Competition and predation both are plausible mechanisms for displacement of cutthroat trout by brook trout.

* Corresponding author: ccmcgrath@fs.fed.us
[1] Present address: U.S. Forest Service, Rocky Mountain Research Station, 322 East Front Street, Suite 401, Boise, Idaho 83702, USA.

Received January 18, 2007; accepted May 11, 2007
Published online August 30, 2007

Competition has been cited as the mechanism by which brook trout displace greenback cutthroat trout (Fausch 1988; Griffith 1988; Adams et al. 2000; Dunham et al. 2002), but few studies have investigated competition between cutthroat trout and brook trout in natural settings. Similarity of feeding behavior and habitat requirements for the two species suggests the potential for both interference and exploitation competition for food between greenback cutthroat trout and brook trout. Competition can be demonstrated only through some measurable effect of sympatry on one or both species. Examples include a niche shift leading to resource partitioning, or a reduction in abundance, density, or body condition of one or both species (Nilsson 1967; Pianka 1981; Ross 1986).

For drift-feeding salmonids, which establish size-based hierarchies, competition for habitat space and food cannot easily be separated experimentally. Because of the coupling of habitat space with food consumption and metabolic expenditures, competition for habitat space often is approached indirectly through estimation of feeding efficiency and growth of species living in sympatry and in allopatry. Such studies suggest that competition between cutthroat trout and brook trout is important. Cutthroat trout and brook trout segregate spatially when sympatric (Griffith 1972, 1974; Novinger 2000). Brook trout display more agonistic behavior and occupy preferred feeding positions (de Staso and Rahel 1994; Novinger 2000), and cutthroat trout shift to more energetically profitable positions when brook trout are removed (Cummings 1987).

Only three published studies give information on the diets of both cutthroat trout and brook trout in natural settings. Griffith (1974) reported that young-of-year (hereafter, age-0) brook trout and westslope cutthroat trout *O. c. lewisi* did not partition food resources in small streams in Idaho. Among older fish, interspecific differences in prey intensified; brook trout used both benthic and drifting foods and gained more weight than sympatric westslope cutthroat trout, which used only drift. In contrast, dietary overlap was high between Lahontan cutthroat trout *O. c. henshawi* and brook trout (Dunham et al. 2000) and between Bonneville cutthroat trout *O. c. utah* and brook trout (Hilderbrand and Kershner 2004), but both of these studies found that feeding of cutthroat trout was probably not limited by brook trout.

Past studies on predation indicate that brook trout can eat greenback cutthroat trout, but it is not clear whether the displacement of greenback cutthroat trout occurs in this way. Age-0 brook trout maintain a size advantage of 20–25 mm over cutthroat trout (Griffith 1972; Novinger 2000). Gape-width models indicate that age-0 brook trout can consume age-0 cutthroat trout and, in a field enclosure study, age-0 greenback cutthroat trout experienced high mortality from predation or injuries related to attacks by age-0 brook trout (Novinger 2000). Gregory and Griffith (2000) attributed overwinter mortality of age-0 cutthroat trout to predation by age-0 brook trout in enclosures, but they did not observe predation directly. Dunham et al. (2000) did not observe predation of Lahontan cutthroat trout by brook trout, but their field study was of limited scope. Griffith (1970) found three prey fish in the stomachs of 311 brook trout and two prey fish in the stomachs of 225 cutthroat trout. He did not report the species of prey fish or whether they were found within allopatric or sympatric populations. Replicated studies conducted under natural conditions are lacking, and the importance of predation by brook trout on cutthroat trout remains uncertain.

Most feeding and growth studies with cutthroat trout have been conducted in the laboratory. Extrapolating laboratory results to the field has been problematic. For example, Thomas (1996) observed a decrease in feeding efficiency of Colorado River cutthroat trout owing to interference competition from brook trout in laboratory experiments. In a related field experiment, however, growth, diet choice, and biomass of prey consumed by cutthroat trout were not significantly lower when brook trout were present. In a review of research on the effects of introduced salmonids, Fausch (1988) emphasized that, despite widespread introductions of nonnative salmonids, "few investigations provide strong evidence for or against interspecific competition with native species in natural streams." Field experiments under natural conditions could demonstrate more reliably the role of competition in displacement of cutthroat trout by brook trout.

We report the results of a replicated field study that was designed to test three hypotheses: (1) brook trout are associated with declines in greenback cutthroat trout populations, (2) brook trout displace greenback cutthroat trout through competition for food, and (3) brook trout displace greenback cutthroat trout through predation. Hypothesis 1 was tested with new and previously collected population data. Hypothesis 2 was evaluated through analysis of gut contents, body condition, and gut fullness. Gut content analysis on large numbers of fish provided data to test hypothesis 3.

Study Area

Ten sites on eight streams in Colorado were studied from July through October 2000–2002. Eight sites were within Rocky Mountain National Park in the South Platte River drainage and two sites were located

TABLE 1.—Reach descriptions and physical habitat of greenback cutthroat trout and brook trout at 10 study sites in the South Platte River and Arkansas River drainages, Colorado, 2000–2002. Habitat area and volume are reported for the wetted channel during low flow; riparian vegetation can exceed 100% if multiple cover types overlap. (see McGrath 2004 for methods).

Variable	Cony Creek	Roaring River	Lion Lakes Creek	Cache la Poudre River	Hidden Valley Creek	Lower Ouzel Creek	Upper Rock Creek	North Fork Big Thompson River	Upper Ouzel Creek	Lower Rock Creek
Elevation (m)	3,028	2,827	3,218	2,996	2,837	2,926	3,087	3,139	3,040	3,031
Mean July temperature (°C)	9.7	9.9	11.1	10.8	5.3	10.6	10.4	9.2	10.6	10.4
Discharge (m^3/s)	0.29	0.23	0.06	0.1	0.05	0.17	0.15	0.14	0.18	0.17
Gradient (%)	2	4.1	0.5	3.4	5.1	2.1	4.7	4.1	4.3	1.3
Reach length (m)	623	648	427	312	348	297	564	612	367	543
Mean reach width (m)	5.6	5.8	2.3	5.7	2.4	5	4.9	3.3	6.5	5.2
Area (m^2)	3,470	3,744	995	1,171	841	1,473	2,788	2,008	2,376	2,800
Pool volume/reach volume	28	9	10	3	8	16	17	3	39	42
Fish cover, areal (%)	24	53	6	38	26	60	41	43	60	34
Riparian vegetation (% streambank with cover type)										
Coniferous trees	53	16	24	51	31	1	9	54	54	44
Deciduous trees	0	1	0	0	6	0	0	2	0	13
Shrubs	24	14	31	65	30	15	57	8	7	88
Grasses or forbs	49	11	49	35	73	90	29	3	37	45
Substrate composition (%)										
Sand	19	7	14	5	17	18	10	14	13	29
Gravel	47	22	38	21	29	37	18	17	32	34
Cobble	29	39	43	46	46	31	42	36	33	27
Boulder	5	32	5	23	7	14	29	33	22	9
Bedrock	0	0	0	4	0	0	0	0	0	0

near the town of Leadville in the Arkansas River drainage. Sites were selected based on characteristics such as fish species present, presence of geomorphic features thought to limit fish movement into and out of study areas, and accessibility. Some attributes of physical habitat were similar among sites (e.g., elevation, dominant substrate), while other habitat characteristics varied greatly (e.g., percentage pool, fish cover, and riparian vegetation; Table 1). With the exception of Hidden Valley Creek, mean daily temperature at all sites ranged from near 0°C in the winter (November–April) to summer maxima of 10.9–12.5°C. Hidden Valley Creek, which has a spring source, was 1.0–1.5°C in the winter and reached only 6.5°C in the summer (McGrath 2004). Study reaches ranged from 312 to 648 m long and consisted of areas with greenback cutthroat trout only (two sites), brook trout only (two sites), both species (three sites), and both species with experimental removal of brook trout (three sites). No other fish species were found at these sites. Between 1973 and 1996, the eight sites with greenback cutthroat trout were treated chemically to eradicate brook trout and, subsequently, were stocked with greenback cutthroat trout by the U.S. Fish and Wildlife Service (USFWS). Brook trout were detected at six of the eight sites within 3 to 7 years of eradication efforts (Young et al. 2002).

Methods

Are brook trout associated with declines in greenback cutthroat trout populations?—Two-pass backpack electrofishing surveys were conducted annually at each site in 2000 and 2001. Surveys were conducted between July 30 and October 5 at low flows (except in the North Fork Big Thompson River, when storms increased streamflow during surveys in 2000). Species, weight, and total length (TL) were recorded for each fish. During 2001, additional electrofishing surveys were conducted 8–10 weeks after annual surveys at two sites where brook trout were removed to determine whether brook trout had recolonized these reaches.

Number of fish per reach was estimated by the Burnham removal–depletion maximum likelihood estimator (MLE; Zippin 1958; Van Deventer and Platts 1983); abundance in terms of kilograms per hectare also was estimated. Percent brook trout was calculated for each reach as the MLE for brook trout divided by the MLE for both species. Densities were compared with historical records of density at each site where records were available. Information on the error in historical data was not available, although sampling methods were similar (i.e., two- or three-pass electrofishing depletion surveys).

Do brook trout displace greenback cutthroat trout through competition for food?—Gut contents were collected by gastric lavage from about 20 individuals (87–303 mm TL) of each species at each site during the fish surveys of 2000. The diet of age-0 fish was not evaluated; every cutthroat trout and all but four brook trout sampled were greater than 150 mm TL. Gut contents were filtered immediately through an 80-μm filter and preserved in 70% ethanol. Fish were returned to calm pools within the study reach, except at brook trout removal sites.

In preserved gut contents, each invertebrate prey was identified to the family level and was counted as an individual if it had a head and thorax. When family-level identification was not possible, prey were identified to order or class. After taxonomic identification, all gut contents, including dismembered items not identified taxonomically, were categorized as aquatic invertebrate, terrestrial invertebrate, plant, vertebrate (age-0 trout), fish eggs, amorphous organic detritus, or inorganic debris (e.g., gravel, trout teeth). Each class of material was oven-dried at 60°C and weighed.

Within each site, count data for the prey taxa consumed by greenback cutthroat trout and brook trout were compared by use of the multiresponse permutation procedure (MRPP), a nonparametric method that can be used for testing group differences in community composition. The Sorensen distance measure was used because it is appropriate for nonlinear and highly skewed data (McCune and Grace 2002). Taxa identified to class or order were treated statistically as equal to taxa that were identified to family. Trout and trout eggs from gut contents were included in the analysis. Differences in diet between greenback cutthroat trout and brook trout were identified by indicator species analysis (ISA), which employs a Monte Carlo procedure to identify indicator species from abundance of prey taxa in the two trout species and consistency of occurrence of a prey taxon for a given trout species (Dufrene and Legendre 1997; McCune and Grace 2002).

Some partially digested prey items typically identified to family were identified only to order, and a few items from rare families with complex identifying characteristics were identified to order. These orders sometimes were indicator taxa. The MRPP and ISA were repeated after these items were removed from the data set, except when every item within a gut was classified to order.

The total lengths of greenback cutthroat trout and brook trout were compared at sites where the two were sympatric, and the diets of small fish (lower 50% of TL) were compared with the diets of large fish (upper 50% of TL) for each species by MRPP.

The number of taxa consumed (prey richness [S]) and Shannon diversity (H') of prey consumed by greenback cutthroat trout and brook trout were calculated for each site. H' was calculated with equation (1),

$$H' = -\sum p_i \cdot \log_e p_i, \tag{1}$$

where p_i is the fraction of prey occurring in prey taxon i.

Mean body condition, K, was compared for allopatric and sympatric populations of greenback cutthroat trout and brook trout by means of equation (2),

$$K = 10^5 \cdot W/L^3, \tag{2}$$

where W is wet weight in grams and L is TL in millimeters (Schreck and Moyle 1990).

Stomach fullness, F, was calculated as the percent dry weight of stomach contents (excluding plant and inorganic material) relative to the wet weight of the fish (Heroux and Magnan 1996; Morita and Suzuki 1999). Stomach fullness for greenback cutthroat trout and brook trout was compared within each site and was compared for allopatric and sympatric populations of each species.

Do brook trout displace greenback cutthroat trout through predation?—Predation rates were estimated from gut content analysis and from analysis of an additional 162 juvenile brook trout (age 0 and age 1; mean TL $\pm$ SE = 88.5 $\pm$ 3.0 mm) that were obtained during brook trout removal operations at Hidden Valley Creek, the North Fork Big Thompson River, Lower Rock Creek, and Upper Rock Creek in 2001 and 2002. Fish were killed and frozen within 8 h and subsequently thawed, dissected for stomach contents, and examined for evidence of prey fish.

Statistical summary.—For all statistical tests, α = 0.05. Nonparametric statistics were used in cases where the assumptions for parametric statistics were violated. Fish population size was calculated with MicroFish 3.0 software (Van Deventer and Platts 1989). The MRPP and ISA were conducted with PD-Ord 4.3 (MjM Software, Gleneden Beach, Oregon). Comparisons (t-test or Welch analysis of variance [ANOVA]) of S, H', K, and F between greenback cutthroat trout and brook trout were done with JMP (SAS Institute, Cary, North Carolina).

Results

Are Brook Trout Associated with Declines in Greenback Cutthroat Trout Populations?

The size of greenback cutthroat trout and brook trout populations varied widely among research sites. Capture probability varied between sites (mean $\pm$ SD = 0.56 $\pm$ 0.18), and low capture probability sometimes produced high standard error in estimates of population size. At sites with both species, brook trout usually outnumbered greenback cutthroat trout. For both species, the largest individuals captured were 250–300 mm long and rarely weighed more than 200 g. Sites with only one species had both small and large individuals in the population. At sites with both

TABLE 2.—Abundance of greenback cutthroat trout (GBC) and brook trout (BKT) in South Platte River and Arkansas River drainages 2000–2002. Values in parentheses are standard errors. Percent BKT postremoval was based on surveys done in 2001.

Variable		GBC only		BKT only		GBC and BKT			GBC and BKT with BKT removal		
		Cony Creek	Roaring River	Lion Lakes Creek	Cache la Poudre River	Hidden Valley Creek	Lower Ouzel Creek	Upper Rock Creek	North Fork Big Thompson River	Upper Ouzel Creek	Lower Rock Creek
Number of GBC	2000	201	188	0	2	3	31	117	60	58	95
		(9)	(5)		(1)	(0)	(43)	(42)	(29)	(3)	(11)
	2001	257	348	0	0	2	17	34	63	31	72
		(34)	(81)			(0)	(17)	(5)	(4)	(43)	(16)
Number of BKT	2000	0	0	170	196	86	354	416	155	424	52
				(5)	(14)	(5)	(26)	(77)	(134)	(12)	(12)
	2001	0	0	175	185	55	332	222	120	379	55
				(15)	(15)	(1)	(13)	(8)	(15)	(19)	(4)
% BKT	2000	0	0	100	99	97	92	78	72	88	35
	2001	0	0	100	100	96	95	87	66	92	43
% BKT postremoval	2001									90[a]	59
% GBC <120 mm	2000	24	8			0	0	7	6	2	11
	2001	31	10			0	0	23	3	7	15
% BKT <120 mm	2000			8	31	0	22	11	24	13	38
	2001			21	36	2	23	30	34	30	49

[a] Estimate based on number of captures during one electrofishing pass because of ice cover.

species, small brook trout were abundant, but there were few small cutthroat trout (Table 2).

At three sites (the North Fork Big Thompson River, Upper Ouzel Creek, and Lower Rock Creek), all brook trout captured in 2000 were removed from the stream. During population surveys in 2001, many brook trout were captured from these sites. Surveys at two of the sites (Upper Ouzel Creek and Lower Rock Creek) indicated that brook trout had recolonized and were predominant at the sites within 8–10 weeks (Table 2).

At several sites, cutthroat trout had been replaced almost completely by brook trout. Although the date of first detection of brook trout was known, data on density of brook trout at study sites in the past were not available (C. Kennedy, USFWS, personal communication). Where past surveys were done (USFWS 1998), the total density of both species was similar to or higher than past density of cutthroat trout (Figure 1). Among the 10 research sites, the negative linear relationship between density of greenback cutthroat trout and density of brook trout was weak ($r^2 = 0.33$, $P = 0.08$). The relationship was better described by a quadratic function ($y = 24 - 0.2x + 0.004(x - 59)^2$; $r^2 = 0.55$, $P = 0.06$).

Do Brook Trout Displace Greenback Cutthroat Trout through Competition for Food?

Of 296 fish sampled for gut contents, 6 brook trout and 1 greenback cutthroat trout did not contain identifiable prey. In the remaining 289 samples, 9,649 identifiable items were counted. Prey taxa comprised 28 classes or orders, including at least 119 families. Most fish had consumed both terrestrial and aquatic prey, though the proportions of aquatic and terrestrial prey varied among sites. Greenback cutthroat trout consumed a higher number of prey than brook trout (Table 3).

The prey consumed by greenback cutthroat trout and brook trout differed significantly at five of the six sites where the species were living in sympatry (Figure 2). Greenback cutthroat trout and brook trout at Hidden Valley Creek did not differ significantly in diet. Because only three greenback cutthroat trout were sampled for gut contents at Hidden Valley Creek, the test had low power at that site. Prey taxa that differed significantly in the diets of greenback cutthroat trout and brook trout included a wide range of aquatic and terrestrial taxa. Greenback cutthroat trout tended to consume more prey taxa and a higher number of items within each prey taxon than brook trout.

In general, the TL of fish sampled for gut contents was similar among sites and between species, but at several sites the brook trout included smaller individuals. At each site, the diets of small and large fish (below and above median TL) within a species did not differ significantly, except for brook trout at Upper Ouzel Creek. At the three sites where there was a significant difference in TL of greenback cutthroat trout and brook trout, small brook trout were removed from the data set until there was no significant difference in size between species at a site. The diets of greenback cutthroat trout and brook trout remained significantly different after trimming at two sites and, at one site (Lower Rock Creek), the difference in diet changed from marginally significant ($P = 0.05$) to not significantly different.

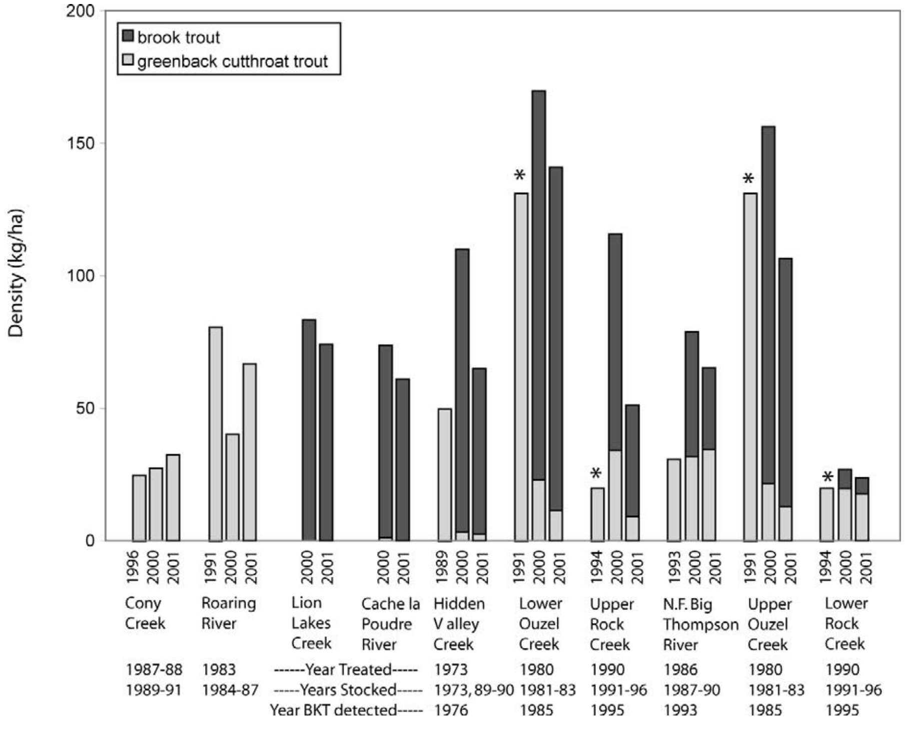

FIGURE 1.—Density of greenback cutthroat trout and brook trout in this study and past reports (USFWS 1998) in the South Platte River and Arkansas River drainages, Colorado. Sites included areas with cutthroat trout only (two sites), brook trout only (two sites), and both species (six sites). Years treated with antimycin, years stocked with greenback cutthroat trout, and year of subsequent detection of brook trout are shown for each site. Data on the density of brook trout are not available prior to 2000. Asterisks denote sites for which a range of densities was reported (midpoints are shown).

The MRPP comparison of the diet of cutthroat trout and brook trout was repeated after removal of a small number of damaged items from the data set. Results differed little from those of the original analysis; analysis of indicator species was not affected by exclusion of items classified as unknown.

The diversity of prey consumed was not significantly different in sympatry than in allopatry for either greenback cutthroat trout or brook trout. At the six sites with both species, greenback cutthroat trout always consumed more prey taxa than did brook trout. At four of the six sites, greenback cutthroat trout

TABLE 3.—Number of brook trout and greenback cutthroat trout sampled (n), mean richness (S) of prey, and Shannon diversity (H') of prey consumed in South Platte River and Arkansas River drainages, 2000–2002. Shannon diversity (site means) did not differ significantly for cutthroat trout or brook trout in allopatry versus sympatry. Asterisks indicate significant difference in H' between cutthroat trout and brook trout in sympatry (t-test).

		Cutthroat trout			Brook trout		
Status	Site	n	S	H'	n	S	H'
Allopatric	Cony Creek	20	11.5	1.99			
	Roaring River	20	14.4	2.08			
	Lion Lakes Creek				19	10.9	1.33
	Cache la Poudre River				20	10.1	1.88
Sympatric	Hidden Valley Creek	3	8.0	1.44	21	7.2	1.56
	Lower Ouzel Creek	13	14.8	2.12	19	4.5	1.13*
	Upper Rock Creek	20	10.6	2.14	17	5.6	1.11*
	North Fork Big Thompson River	19	18.4	2.16	20	8.7	1.63*
	Upper Ouzel Creek	19	11.5	1.65	19	3.7	0.82*
	Lower Rock Creek	20	8.1	1.80	20	7.0	1.63

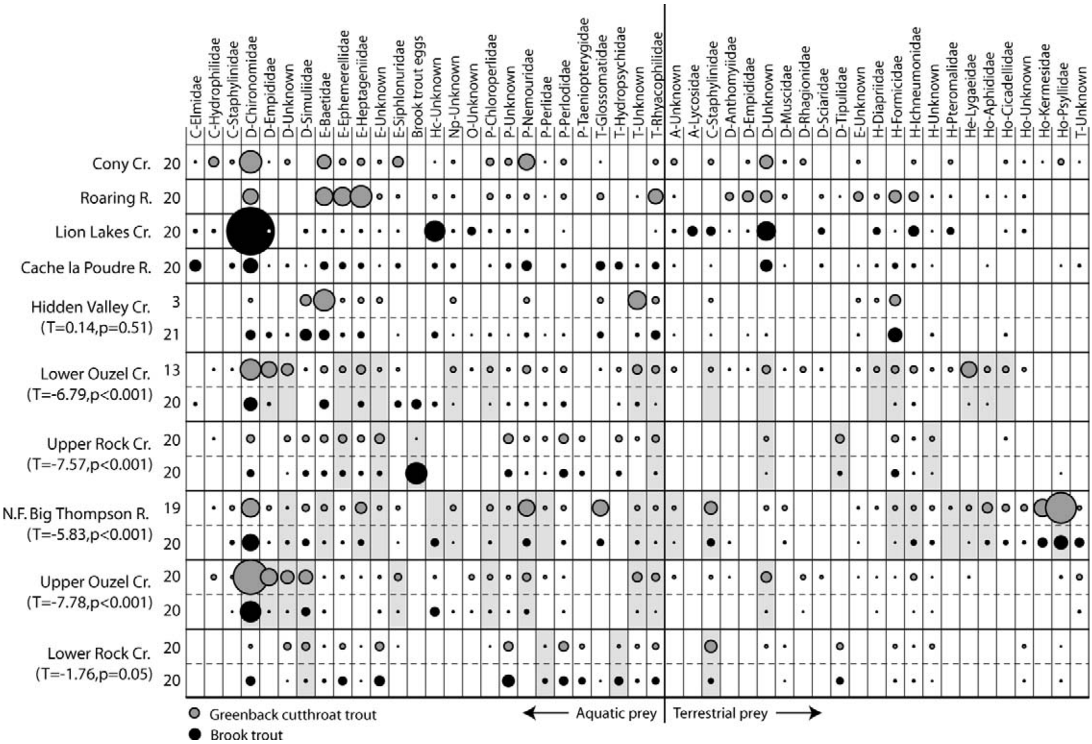

FIGURE 2.—Relative frequency of the 49 most abundant prey taxa in the stomachs of greenback cutthroat trout and brook trout in the South Platte River and Arkansas River drainages, 2000–2002. Not shown are 103 rarer prey taxa found in stomach contents. The area of each bubble represents the number of prey per fish (range = 0.05–44.7). Aquatic and terrestrial life stages are reported separately. The number of trout sampled and the results of multiresponse permutation procedures used to compare the diets of cutthroat trout and brook trout are shown. Background shading indicates significant indicator taxa. Codes for prey class or order are as follows: Araneae (A), Coleoptera (C), Diptera (D), Ephemeroptera (E), Hemiptera (He), Homoptera (Ho), Hymenoptera (H), Hydracarina (Hc), Nematomorpha (Np), Ostracoda (O), Plecoptera (P), and Trichoptera (T).

consumed a significantly higher diversity of prey than did brook trout (t-test: $P = 0.019$ at the North Fork Big Thompson River, $P < 0.001$ at Lower Ouzel Creek, and $P < 0.001$ at Upper Ouzel Creek; Welch ANOVA for unequal variance: $P < 0.001$ at Upper Rock Creek; Table 3).

The gut contents of greenback cutthroat trout and brook trout contained a wide range of food and nonfood items. At some sites, nonfood items (plant and inorganic material) comprised a large proportion of gut contents. The proportionate contributions of food categories to weight of gut contents varied among sites. At a given site, greenback cutthroat trout and brook trout tended to consume similar proportions of food categories, although the intraspecific variability was high. At every site, aquatic invertebrates, terrestrial invertebrates, and amorphous organic detritus were the dominant food items. Trout eggs and age-0 trout also were consumed at some sites (Figure 3).

Nonfood categories were excluded from calculation of F. For both greenback cutthroat trout and brook trout, F varied widely within and between sites. At two sites with the species in sympatry, greenback cutthroat trout had significantly higher F than did brook trout (Figure 3).

Body condition varied from 0.84 for greenback cutthroat trout at Upper Rock Creek and Lower Rock Creek to 1.26 for brook trout at Hidden Valley Creek. The mean body condition for each species was near 1.0 at most sites (cutthroat trout: overall mean = 0.96, SE = 0.02; brook trout: mean = 1.05, SE = 0.03). For both greenback cutthroat trout and brook trout, body condition did not differ significantly between populations living in allopatry and sympatry.

Do Brook Trout Displace Greenback Cutthroat Trout through Predation?

Brook trout had a piscivory rate of 0.3% (one prey fish in the stomach of 1 out of 323 brook trout). The prey fish was identified as an age-0 greenback cutthroat

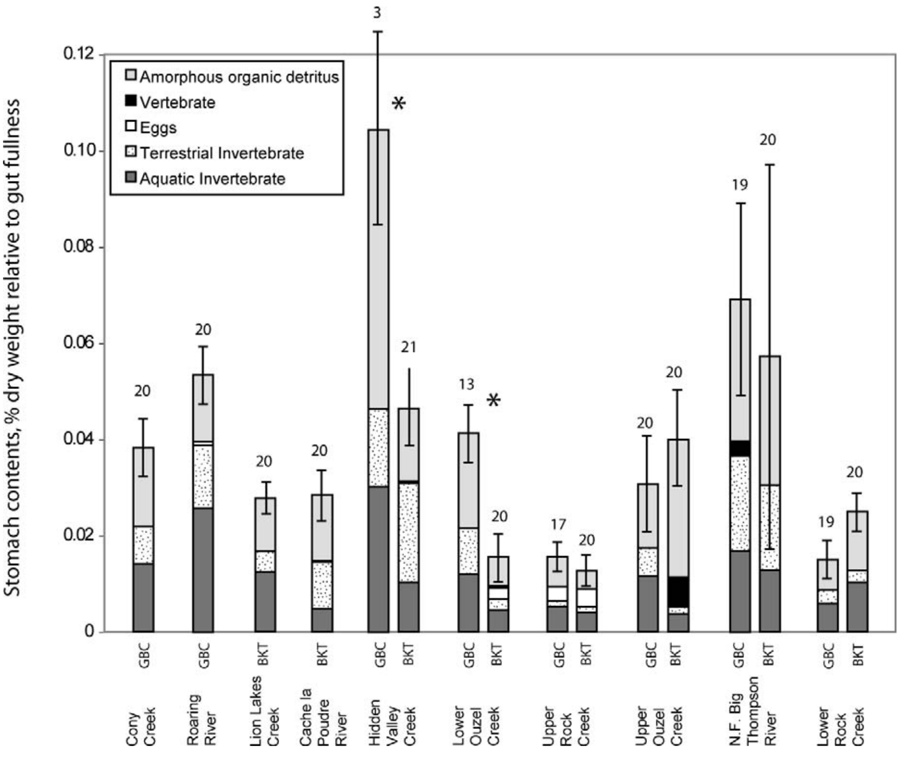

FIGURE 3.—Mean proportional weights of food categories in stomachs of greenback cutthroat trout (GBC) and brook trout (BKT) in the South Platte River and Arkansas River drainages, 2000–2002. The height of each bar represents the mean value of the fullness index; the vertical lines represent SEs. The number of fish sampled is indicated above each bar. Asterisks denote significant differences in fullness between greenback cutthroat trout and brook trout.

trout. Greenback cutthroat trout had a predation rate of 2.9% (four prey fish in the stomachs of 3 out of 136 greenback cutthroat trout). Three of the four prey fish found in greenback cutthroat trout were age-0 cutthroat trout (from Roaring River, where brook trout were not present); the identification of the fourth prey fish was uncertain.

Discussion

Are Brook Trout Associated with Declines in Greenback Cutthroat Trout?

The higher density of brook trout and lower density of greenback cutthroat trout at sites where the species occurred in sympatry (Figure 1) were anticipated, given the results from past studies (Dunham et al. 2003; Novinger and Rahel 2003; Peterson et al. 2004). Only at Lower Rock Creek did greenback cutthroat trout outnumber brook trout, possibly because of more recent stocking of cutthroat trout (Figure 1) or higher rates of brook trout removal by fishermen at the request of nearby fish hatchery personnel (C. Martinez, USFWS, personal communication).

The recovery criteria for sites with greenback cutthroat trout (USFWS 1998) include a biomass of at least 22 kg/ha maintained by natural reproduction and exclusion of nonnative salmonids by a natural or artificial barrier. The sites in this study supported 25.4–155.4 kg/ha of both trout species (Figure 1). If brook trout were eradicated from these sites, each of these sites probably could support at least 22 kg/ha of greenback cutthroat trout, but greenback cutthroat trout probably would not maintain densities as high as the total density of greenback cutthroat and brook trout in sympatry. The present study and other studies (Fausch 1988; Griffith 1988; Dunham et al. 2000) have shown that population density tends to be higher for brook trout than for cutthroat trout. According to Schroeter (1998), the behavioral responses of cutthroat trout to high densities of brook trout may be energetically expensive and, as a result, cutthroat trout may be less able to defend territories. The results of the present study are contradictory to Schroeter's hypothesis that cutthroat trout have unimpaired body condition in sympatry with brook trout.

Do Brook Trout Displace Greenback Cutthroat Trout through Competition for Food?

Considerable overlap in diet may occur, even when foods are partitioned among fish species (Gerking 1994), but there is no significant evidence for dietary partitioning among age-2 and older fish in the present study. Sympatry did not affect prey diversity for greenback cutthroat trout or brook trout. Past descriptions of diet for cutthroat trout and brook trout, though less extensive than those of the present study, also demonstrated no differences in diet between sympatric and allopatric populations of cutthroat trout (Griffith 1970; Thomas 1996) and present no evidence that brook trout limit feeding by cutthroat trout (Dunham et al. 2000; Hilderbrand and Kershner 2004). Neither stomach fullness nor body condition differed between greenback cutthroat trout and brook trout in allopatry and sympatry, and body condition data indicate that most fish at these sites were healthy (Carlander 1969). These results indicate that exploitative competition was not occurring and that food was not a limiting resource in these streams. Interference competition for food, which can occur even if food is not limiting, was not observed and, if it did occur, had no effect on body condition. These findings also are supported by Novinger and Rahel (2003), who found that abundance and body condition of Colorado River cutthroat trout did not increase significantly after removal of brook trout.

The diets of both species varied greatly among sites (Figure 2). The realized trophic niche of greenback cutthroat trout was wider than that of brook trout, as evidenced by the S and H' values of the prey consumed. Because H' did not differ for either species in allopatry versus sympatry, the difference in trophic niche breadth between cutthroat trout and brook trout probably reflects a difference in feeding behavior inherent to these two species rather than response to competition.

Do Brook Trout Displace Greenback Cutthroat Trout through Predation?

The results of past studies on predation are conflicting (Griffith 1970; Dunham et al. 2000; Gregory and Griffith 2000; Novinger 2000), but none provide statistically valid evidence that predation by brook trout accounts for declines in the populations of cutthroat trout. In the present study, rates of piscivory were low for both greenback cutthroat trout and brook trout. The tendency of brook trout to prey on their own eggs suggests that they also prey on eggs of greenback cutthroat trout, which could affect recruitment of greenback cutthroat trout when brook trout are present at high densities. Data from all seasons would strengthen the evaluation of piscivory. In a related study, McGrath (2004) used stable isotope analysis to show that the two species occupied a similar trophic level, which agrees with the results of stomach content analysis. Piscivory is rare, at least during the ice-free season, and predation is probably not the major mechanism for displacement of greenback cutthroat trout by brook trout.

An important limitation of this study is that analyses were conducted mainly on individuals age 2 or older. Because gastric lavage on fish smaller than 150 mm TL is inefficient and can be lethal, greenback cutthroat trout under 150 mm were not examined. The population data suggest that the major effect of brook trout is on juvenile greenback cutthroat trout, so it is possible that competition for food between juvenile greenback cutthroat trout and juvenile brook trout is an important mechanism for displacement of greenback cutthroat trout.

Population-Level Processes Related to Displacement of Cutthroat Trout by Brook Trout

The invasion of brook trout occurs through net immigration and reproduction. Brook trout are highly mobile and tend to move upstream, particularly during early summer and early fall (Gowan and Fausch 1996; Adams et al. 2000; Peterson and Fausch 2003). Peterson and Fausch (2003) removed brook trout from a stream segment where Colorado River cutthroat trout lived, but brook trout repopulated the segment from downstream within 8 months. In the present study, brook trout recolonized three sites within 8–10 weeks of removal. Recruitment also was successful for brook trout. Brook trout smaller than 120 mm TL were well represented in population surveys, indicating reproduction and survival of juvenile brook trout.

Population data showed lower numbers of juvenile greenback cutthroat trout at sites with brook trout than at sites where brook trout were not present. The low numbers of juvenile greenback cutthroat trout probably reflect low survival of eggs and juveniles rather than reproductive failure of adults because body condition of mature greenback cutthroat trout was not affected by brook trout, indicating that fecundity of greenback cutthroat trout probably is not impaired by presence of brook trout. Direct competition for spawning habitat is unlikely because the two species spawn months apart. Both species prey on brook trout eggs, but the importance of predation by brook trout on greenback cutthroat trout eggs could not be determined because stomach content samples were not taken during the season when cutthroat trout eggs are available and vulnerable to predation.

Juvenile greenback cutthroat trout experience higher rates of mortality in the presence of brook trout. Peterson et al. (2004) confirmed a negative relationship between survival of juvenile cutthroat trout and density of juvenile brook trout, but no relationship between survival of age-2 and older cutthroat trout and density of age-2 and older brook trout. Similarly, Hilderbrand (2003) used stage-structured demographic models to show that the two most important elements affecting population growth rate for cutthroat trout were survival of juveniles that became reproductively mature the next year and survival of age-0 fish.

Another possible explanation for the loss of juvenile greenback cutthroat trout is net emigration from restoration sites because of poor habitat conditions or agonistic interactions with brook trout. Studies of other subspecies of cutthroat trout have produced variable results, including (1) net movement downstream (Schmetterling 2000; Peterson and Fausch 2003), (2) net movement upstream (Hilderbrand and Kershner 2000), (3) movement both downstream and upstream in seasonal cycles (Peterson and Fausch 2002), and (4) no net directional movement (Young 1996). Most of these studies focused on fish age 2 and older.

When brook trout are present, the major effect on greenback cutthroat trout apparently occurs in age-0 fish. Possible mechanisms for displacement include (1) competition for food among juvenile fish, (2) behavioral aggression, which may cause age-0 cutthroat trout to occupy suboptimal habitat or to emigrate downstream, (3) predation on age-0 fish during the winter, and (4) predation on cutthroat trout eggs. Measurement of feeding, growth, and lipid levels in age-0 fish in the field would provide insight into these potential mechanisms. Furthermore, habitat-related disturbances that might encourage replacement of cutthroat trout by brook trout (e.g., brook trout invasion after cutthroat trout have declined for other reasons) should be evaluated as possibly explaining declines in cutthroat trout at particular sites.

For endangered species, it has become standard practice for biologists to assume that some type of habitat requirement is the focus of competition as a native and an invasive species attempt to occupy the same habitat. The present study shows that the mechanism leading to the loss of native cutthroat trout living in sympatry with nonnative brook trout is probably not related to the inferior competitive ability of adults involving habitat or food, even though the two species overlap strongly in their use of these resources. Rather, brook trout impose a bottleneck on the recruitment of age-0 cutthroat trout for a brief interval of their life history. Outside of this vulnerable period, cutthroat trout appear to be unaffected by brook trout.

Acknowledgments

We thank Chris Kennedy, James McCutchan, Andrea Noble, Bruce Rosenlund, James Saunders, and Harold Tyus for their assistance with this research and two anonymous reviewers who provided insightful comments on the manuscript. Funding was provided by the Leslie Fidel Bailey Fellowship Program of the Rocky Mountain Nature Association and Rocky Mountain National Park; the North American Native Fishes Association; Ocean Journey of Colorado; the Colorado Mountain Club; and the Graduate School, Cooperative Institute for Research in Environmental Sciences, and Department of Ecology and Evolutionary Biology at the University of Colorado in Boulder.

References

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2000. Movements of nonnative brook trout in relation to stream channel slope. Transactions of the American Fisheries Society 129:623–638.

Allendorf, F. W., R. F. Leary, P. Spruell, and J. K. Wenburg. 2001. The problems with hybrids: setting conservation guidelines. Trends in Ecology and Evolution 16:613–622.

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

Bulkley, R. V. 1959. Report on 1958 fishery studies by the Bureau of Sport Fisheries and Wildlife in Rocky Mountain National Park. U.S. Department of the Interior, Logan, Utah.

Carlander, K. D. 1969. Handbook of freshwater fishery biology, volume 1. Life history data on freshwater fishes of the United States and Canada, exclusive of Perciformes. Iowa State University Press, Ames.

Cummings, T. R. 1987. Brook trout competition with greenback cutthroat trout in Hidden Valley Creek, Colorado. Master's thesis. Colorado State University, Fort Collins.

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

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345–366.

Dunham, J. B., S. B. Adams, R. E. Schroeter, and D. C. Novinger. 2002. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. Reviews in Fish Biology and Fisheries 12:373–391.

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

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

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.

Gerking, S. D. 1994. Feeding ecology of fish. Academic Press, New York.

Gowan, C., and K. D. Fausch. 1996. Mobile brook trout in two high-elevation Colorado streams: reevaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370–1381.

Gregory, J. S., and J. S. Griffith. 2000. First-winter survival of caged wild and hatchery cutthroat trout in allopatry and in sympatry with brook trout. Intermountain Journal of Sciences 6:217–222.

Griffith, J. S., Jr. 1970. Interaction of brook trout and cutthroat trout in small streams. Doctoral dissertation. University of Idaho, Moscow.

Griffith, J. S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada 29:265–273.

Griffith, J. S., Jr. 1974. Utilization of invertebrate drift by brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in Idaho. Transactions of the American Fisheries Society 3:440–447.

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

Heroux, D., and P. Magnan. 1996. In situ determination of food daily ration in fish: review and field evaluation. Environmental Biology of Fishes 46:61–74.

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

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

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

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon.

McGrath, C. C. 2004. Trophic roles of native greenback cutthroat trout and nonnative brook trout in montane streams of Colorado. Doctoral dissertation. University of Colorado, Boulder.

Morita, K., and T. Suzuki. 1999. Shifts of food habitat and jaw position of white-spotted charr after damming. Journal of Fish Biology 55:1156–1162.

Nilsson, N. A. 1967. Interactive segregation between fish species. Pages 295–313 *in* S. D. Gerking, editor. The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford, UK.

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

Novinger, D. C., and F. J. Rahel. 2003. Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. Conservation Biology 17:772–781.

Peterson, D. P., and K. D. Fausch. 2002. Demography, dispersal, and effects of nonnative brook trout on native cutthroat trout in Colorado streams. Department of Fishery and Wildlife Biology, Colorado State University. Final Project Report submitted to Central Utah Project Completion Act Office (U.S. Department of the Interior), Colorado Division of Wildlife, U.S. Forest Service, and Trout Unlimited, Fort Collins, Colorado.

Peterson, D. P., and K. D. Fausch. 2003. Upstream movement by nonnative brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Oncorhynchus clarki*) habitat. Canadian Journal of Fisheries and Aquatic Sciences 60:1502–1516.

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

Pianka, E. R. 1981. Competition and niche theory. Pages 167–196 *in* R. M. May, editor. Theoretical ecology. Sinauer, Sunderland, Massachusetts.

Ross, S. T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 1986:352–388.

Schmetterling, D. A. 2000. Seasonal movements of fluvial westslope cutthroat trout in the Blackfoot River drainage, Montana. North American Journal of Fisheries Management 20:711–719.

Schreck, C. B., and P. B. Moyle. 1990. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Schroeter, R. E. 1998. Segregation of stream-dwelling Lahontan cutthroat trout and brook trout: patterns of occurrence and mechanisms for displacement. Master's thesis. University of Nevada, Reno.

Thomas, H. M. 1996. Competitive interactions between a native and exotic trout species in high mountain streams. Master's thesis. Utah State University, Logan.

Trotter, P. C. 1987. Cutthroat: native trout of the West. Colorado Associated University Press, Boulder.

USFWS (U.S. Fish and Wildlife Service). 1998. Greenback cutthroat trout recovery plan. USFWS, Denver.

Van Deventer, J. S., and W. S. Platts. 1983. Sampling and estimating fish populations from streams. Transactions of the North Amercian Wildlife and Natural Resources Conference 48:349–354.

Van Deventer, J. S., and W. S. Platts. 1989. Microcomputer software system for generating population statistics from electrofishing data: user's guide for MicroFish 3.0. U.S. Forest Service General Technical Report INT-254.

Young, M. K. 1995. Conservation assessment for inland cutthroat trout. U.S. Forest Service General Technical Report RM-256.

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

Young, M. K., and A. L. Harig. 2001. A critique of the recovery of greenback cutthroat trout. Conservation Biology 15:1575–1584.

Young, M. K., A. L. Harig, B. Rosenlund, and C. Kennedy. 2002. Recovery history of greenback cutthroat trout: population characteristics, hatchery involvement, and bibliography. U.S. Forest Service, RMRS-GTR-99WWW, Fort Collins, Colorado.

Zippin, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22:82–90.