Transactions of the American Fisheries Society 115:382–391, 1986

Production and Habitat of Threatened Greenback and Colorado River Cutthroat Trouts in Rocky Mountain Headwater Streams

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Abstract.—Field studies conducted in 1979 and 1980 to assess the production and habitat of cutthroat trouts *Salmo clarki* in three headwater tributaries in north-central Colorado yielded the following estimates of production (g/m^2): greenback cutthroat trout *S. c. stomias* in Roaring Creek, 3.3 in 1979 and 2.3 in 1980; greenback cutthroat trout in the Right Hand Fork of Roaring Creek, 3.6 in 1979 and 1.5 in 1980; Colorado River cutthroat trout *S. c. pleuriticus* in Little Green Creek, 2.2 in 1979 and 3.6 in 1980. Biomass and production in Roaring Creek and Right Hand Fork of Roaring Creek were dominated by old ($\geq$3 years) slow-growing fish. Little Green Creek was the warmest and slowest moving of the creeks studied and had a low diversity of substrates dominated by fine and coarse gravel—it also had the highest biomass and production of young of the year. Right Hand Fork Roaring Creek had faster flows and more extensive undercut banks—it also had the most large fish ($\geq$152 mm long). Biomass and production of cutthroat trout within the three streams depended mainly on stream-specific physical characteristics. In addition, year-class strength appeared to be mainly affected by the time of emergence and growth rates of juveniles prior to their first winter and by the abundance of large resident fish.

The greenback cutthroat trout *Salmo clarki stomias* and Colorado River cutthroat trout *S. c. pleuriticus* are two of several rare subspecies of cutthroat trouts native to high-elevation streams in western North America. The greenback cutthroat trout is native to the South Platte and Arkansas river basins in Colorado and Wyoming, and the Colorado River cutthroat is native to upper tributaries of the Colorado River in Colorado, Wyoming, New Mexico, and Utah (Langlois et al. 1977; Behnke and Benson 1980). In the past 100 years, nearly all stocks of both subspecies have suffered one of three fates: (1) extirpation because of habitat destruction resulting from mining, irrigation diversions, or grazing (Langlois et al. 1977); (2) extirpation because of unsuccessful competition with introduced stocks of fall-spawning brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta*; or (3) hybridization with introduced stocks of cutthroat trout and rainbow trout *Salmo gairdneri* (Behnke and Benson 1980). The greenback cutthroat trout is classified as "threatened" by the U.S. Department of the Interior and both subspecies are classified as threatened by the state of Colorado.

Knowledge of the production (growth in weight by all individuals during a specified time period, including fish dying during that period) and habitat of these subspecies should aid biologists in managing the remaining stocks and in establishing new ones. The basic life histories of both subspecies have been investigated (Bulkley 1959; Drummond 1966), but there have been no studies of the production of either subspecies, and apparently only one investigation into factors affecting production. In that study, Drummond and McKinney (1965) found that recruitment of juveniles into Trapper's Lake, Colorado, was inversely related to the amount of snowpack during the preceding winter.

Our objectives were to (1) assess the production of greenback and Colorado River cutthroat trouts in three small tributaries in northern Colorado, (2) characterize their habitats, and (3) relate habitat conditions within streams and differences between streams to the production.

Study Sites

The three tributaries studied were in north-central Colorado (Figure 1; Scarnecchia 1983). Angling pressure on the three tributaries has not been quantified but appears to be low. Roaring Creek originates in the Roosevelt National Forest and flows into the Cache la Poudre River near the town of Kinikinik. Two sections of Roaring Creek were studied. The study site on the Right Hand Fork

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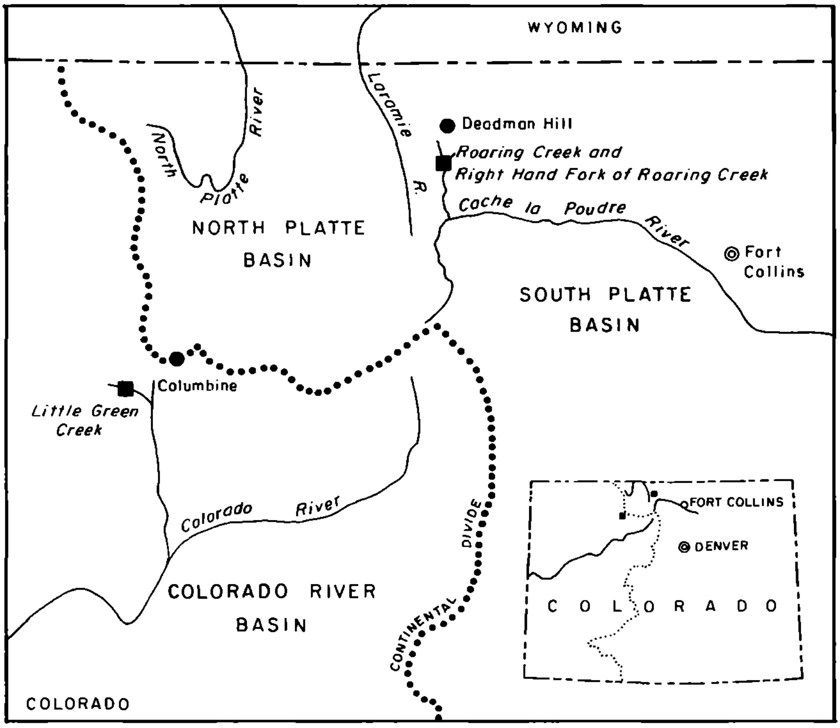

FIGURE 1.—Locations of three sections of streams in which production of cutthroat trout was investigated. Columbine and Deadman Hill are stations where snowpack was measured.

of Roaring Creek, designated Right Fork (first order) was 3,139 m above sea level and 200 m long. During midsummer, an average discharge was 0.02 m^3/s and mean width was 1.6 m. The small, closely confined channel resulted from the confluence of many rivulets draining the wet meadow above. The upper half of the section was heavily shaded by willows *Salix* sp., and the lower half by lodgepole pine *Pinus contorta* and Engelmann spruce *Picea engelmanni*.

Our second study site, on Roaring Creek (second order), was 2 km downstream from Right Fork. The section was 2,987 m above sea level and 200 m long. During midsummer, mean discharge was 0.075 m^3/s and mean width 3.1 m. The channel was less shaded and less confined than that of Right Fork; it traversed open meadows containing scattered lodgepole pines and willows.

In both sections, greenback cutthroat trout was the only species of fish present. R. J. Behnke (Colorado State University, unpublished) quantified taxonomic characters of Roaring Creek cutthroat trout, and considered them to be slightly hybridized with introduced *Salmo,* but still one of several "good representatives" of the subspecies. Although we did not evaluate taxonomic differences between fish of these two sections, we observed that individual fish from Right Fork, the higher section, appeared more distinctive from hatchery-reared cutthroat and rainbow trout stocks than did fish from Roaring Creek.

Little Green Creek is a second-order headwater tributary of the Colorado River, and flows near Rabbit Ears Pass on the Continental Divide. The section studied was 2,807 m above sea level and 200 m long. During midsummer, mean discharge in the section was 0.009 m^3/s and mean width was 1.5 m. Tall grasses along the banks shaded the watercourse, which was deeply incised into the surrounding meadow. Cutthroat trout was the only species of fish present. Wagner and Chapal (Colorado Division of Wildlife, unpublished) characterized these fish, based on morphology, meristic and spotting patterns, as a pure or essentially pure genetic stock of Colorado River cutthroat trout.

Methods

Population estimates.—We sampled with backpack electrofishing units in each of the three sections, twice in 1979 and three times in 1980 (Table

1). Before the sampling, each section was blocked at upper and lower ends with fine-meshed seine nets. We estimated abundance of cutthroat trout by the three-pass removal method (Zippin 1956, 1958) from the y-intercept of the regression of catch in the ith pass (x) on previous total catch (y). Population sizes were estimated separately forage-0 fish when sufficient sample sizes permitted it, but fish aged 1 and older were grouped for population estimation. The total population estimate was then partitioned back into separate ages in proportion to the number of fish caught of each age. Because of this grouping, confidence intervals about the population estimates are not very meaningful; however, we were able to capture over 80% of the estimated population of age-0 fish and over 97% of the estimated number of age-1 and older fish. Captured fish were retained temporarily in fine-meshed permeable baskets placed at intervals along each section. Lengths and weights were recorded from all fish except some groups of young of the year, which we only subsampled. For each section, the densities of fish equaling or exceeding 152 mm and 202 mm in total length were calculated from the average value of the population estimates and expressed as the number of fish of at least that length per unit of surface area. After we had obtained the required data, we returned each fish, when possible, to the pool or riffle from which it had been removed.

The ages of fish were determined mainly from length-frequency distributions and scale analysis (Brown and Bailey 1952; Tesch 1971; Scarnecchia 1983). For fish aged 3 and younger, length modes were correlated closely with the number of clear annuli on scales. During the last population estimate in 1980, a small sample of otoliths was obtained from fish of Roaring Creek. Otoliths were prepared in glycerine and interpreted as outlined by Williams and Bedford (1974).

During the first population estimates for all three sections, a sample of fish longer than 135 mm was branded with silver-tipped branding irons (Groves and Novotny 1965). We used a coding system based on binary numbers to enable us to subsequently identify recaptured fish. During the second sampling of the streams, some previously unbranded fish were branded. During the second and subsequent three samplings, branded fish were recovered, identified, measured for length, and weighed.

Production estimates.—Population sizes (N) and average weights (W) by age of cutthroat trout could be estimated satisfactorily during summer and early autumn, but not during winter nor during periods of high runoff in spring. Data on weights (Table 1) indicated that fish grew rapidly during May and June and we needed to estimate production for such periods. To estimate this production, we assumed that fish did not grow from November 1 until April 30. Mortality rates of all age classes over winter were assumed to be exponential. Any deviations from exponential growth over winter would not substantially alter production estimates anyway if growth rates were low over winter. For both 1979 and 1980, population sizes and average weights were estimated for October 31 and April 30 based on assumptions of steady-state growth and mortality, and on yearly growth and mortality trends.

The ages of cutthroat trout could not be accurately determined with scales or otoliths beyond age 4. For these fish, we assumed that annual growth in grams was equal to that of similarly sized branded fish in that stream, as judged by weights of branded fish recaptured on successive sampling dates.

Annual (January–December) production (g/m^2) for each age class and stream was calculated as $P = G\bar{B}$ (Ricker 1946). The instantaneous rate of growth G is calculated as $\log_e W_t - \log_e W_0$, where W_0 and W_t are initial and final weights, respectively, for each time interval between samplings; $\bar{B}$ is the average biomass over the interval t for which G is constant. Values for $\bar{B}$ were calculated as $\bar{B} = B_0[e^{(G-Z)} - 1]/[G - Z]$ (Ricker 1975), where B_0 is the biomass at the beginning of the interval. The instantaneous rate of natural mortality, Z, is calculated as $\log_e N_0 - \log_e N_t$ where N_0 and N_t are initial and final weights, respectively, for each time interval between samplings. Annual average biomass for each stream each year was computed as the arithmetic average of $\bar{B}$ values between sampling intervals.

Habitat measurements.—Several physical characteristics of each section were measured once in 1979 and once in 1980, between August 1 and October 31. In each section, a horizontal transect perpendicular to the flow was established at the downstream end of the section and every 20 m upstream to the other end of the section. Across each transect, seven equidistant stations were established, the fourth of which was in the center of the stream (Stewart 1970), so that each section had 11 transects and 77 stations.

We measured width of the stream at each transect. At each station, we measured the depth and evaluated the substrate visually by particle size

TABLE 1.—Estimates of population size (*N*) and average weights per fish (*W*) in grams for greenback and Colorado River cutthroat trout in Roaring Creek, Right Fork, and Little Green Creek in 1979 and 1980. Italic values were indirectly calculated or assumed.

Date	Variable	Age 0	1	2	3	4	5 and older
Roaring Creek: greenback cutthroat trout							
1979							
May 1	*N*	*0*	*35*	*60*	*60*	*30*	*14*
	W	*0.0*	*0.9*	*5.0*	*13.0*	*29.0*	*47.5*
Jul 31–	*N*	0	25	55	56	27	14
Aug 1	*W*	0.0	1.7	15.3	23.0	45.5	68.3
Sep 25–	*N*	271	23	42	66	23	18
26	*W*	0.3	3.8	12.7	27.8	43.5	69.0
Oct 31	*N*	*179*	*21*	*42*	*59*	*21*	*18*
	W	*0.4*	*4.0*	*13.0*	*28.0*	*43.5*	*69.0*
1980							
May 1	*N*	*0*	*24*	*13*	*48*	*35*	*33*
	W	*0.0*	*0.4*	*4.0*	*12.7*	*28.0*	*53.6*
Jul 9–10	*N*	0	11	11	48	29	31
	W	0.0	1.0	4.7	12.7	29.9	55.4
Aug 27–	*N*	545	18	22	59	48	20
28	*W*	0.08	4.3	10.2	24.3	38.6	62.6
Oct 2–4	*N*	505	29	31	53	55	24
	W	0.3	4.7	12.2	22.9	35.7	55.9
Oct 31	*N*	*474*	*29*	*28*	*50*	*55*	*24*
	W	*0.9*	*4.7*	*12.2*	*22.9*	*35.7*	*55.9*
Right Hand Fork Roaring Creek: greenback cutthroat trout							
1979							
May 1	*N*	*0*	*10*	*7*	*8*	*35*	*29*
	W	*0.0*	*0.3*	*2.7*	*8.1*	*19.3*	*49.8*
Aug 2	*N*	0	3	7	5	33	24
	W	0.0	1.0	7.3	15.4	42.3	61.8
Sep 1–2	*N*	0	3	11	8	28	23
	W	0.0	2.7	8.1	19.3	40.5	65.8
Oct 31	*N*	*0*	*3*	*10*	*7*	*26*	*25*
	W	*0.0*	*2.7*	*8.1*	*19.3*	*40.5*	*65.3*
1980							
May 1	*N*	*0*	*0*	*3*	*9*	*6*	*37*
	W	*0.0*	*0.0*	*2.7*	*8.1*	*19.3*	*50.1*
Jul 11–	*N*	0	0	3	8	5	33
12	*W*	0.0	0.0	10.7	15.1	29.4	53.3
Aug 24	*N*	5	6	6	13	15	30
	W	0.1	3.3	10.3	19.8	36.3	68.8
Sep 30	*N*	76	9	4	14	7	20
	W	0.1	3.8	8.8	19.4	41.0	61.3
Oct 31	*N*	*70*	*9*	*4*	*14*	*6*	*20*
	W	*0.3*	*3.8*	*8.8*	*19.4*	*41.0*	*61.3*
Little Green Creek: Colorado River cutthroat trout							
1979							
May 1	*N*	*0*	*10*	*20*	*9*	*17*	*4*
	W	*0.0*	*0.7*	*6.2*	*13.5*	*30.8*	*45.5*
Aug 7	*N*	13	8	14	9	17	3
	W	0.1	2.6	15.4	23.6	42.1	54.0
Sep 16	*N*	158	6	9	5	15	2
	W	0.4	6.2	17.2	30.8	45.5	45.0
Oct 31	*N*	*129*	*6*	*9*	*5*	*15*	*2*
	W	*0.5*	*6.2*	*17.2*	*30.8*	*45.5*	*45.0*
TABLE 1.—Continued.							
1980							
May 1	*N*	*0*	*58*	*10*	*14*	*10*	*14*
	W	*0.0*	*0.5*	*6.2*	*13.5*	*30.8*	*45.5*
Jul 23	*N*	0	40	10	14	10	13
	W	0.0	3.3	11.9	25.8	37.5	48.5
Sep 11–	*N*	378	18	1	11	9	2
12	*W*	0.7	4.9	15.0	29.2	47.0	43.0
Oct 10–	*N*	489	9	5	7	8	2
11	*W*	0.9	4.9	13.5	32.2	42.6	48.0
Oct 31	*N*	*400*	*9*	*5*	*7*	*8*	*2*
	W	*1.0*	*5.0*	*13.5*	*32.2*	*42.6*	*48.0*

according to a modified Wentworth classification. Diversity of substrates was later estimated with the Shannon–Weiner index (Pielou 1975). Velocity was measured at 0.6 of the depth (Stalnaker and Arnette 1976) with an Ott[3] Model C2 current meter.

Only one aspect of cover was measured—the quantity of undercut banks. We measured the along-stream length of any section of streambank that was cut at least 20 cm into the bank and covered with water at least 10 cm deep. All such lengths of undercut banks were summed for each section of stream and the results were exposed as centimeters of undercut bank per meter of stream.

The maximum temperature of the water during the summer period was measured in each section with maximum–minimum thermometers. Conductivity was measured with a Beckman RB 3 Solubridge calibrated with potassium chloride standard solutions (APHA et al. 1975).

In order to investigate the relation between winter snowpack and production of specific year classes (Drummond and McKinney 1965), information on snowpack (snow water content) in the proximity of the three streams during winter and spring from 1975 to 1981 was obtained from the U.S. Soil Conservation Service (1975–1981) at the Columbine and Deadman Hill sites (Figure 1).

Results

Fish Production

Roaring Creek.—Both production and biomass of greenback cutthroat trout in Roaring Creek were

[3] Reference to trade names or manufacturers does not imply U.S. Government endorsement of products.

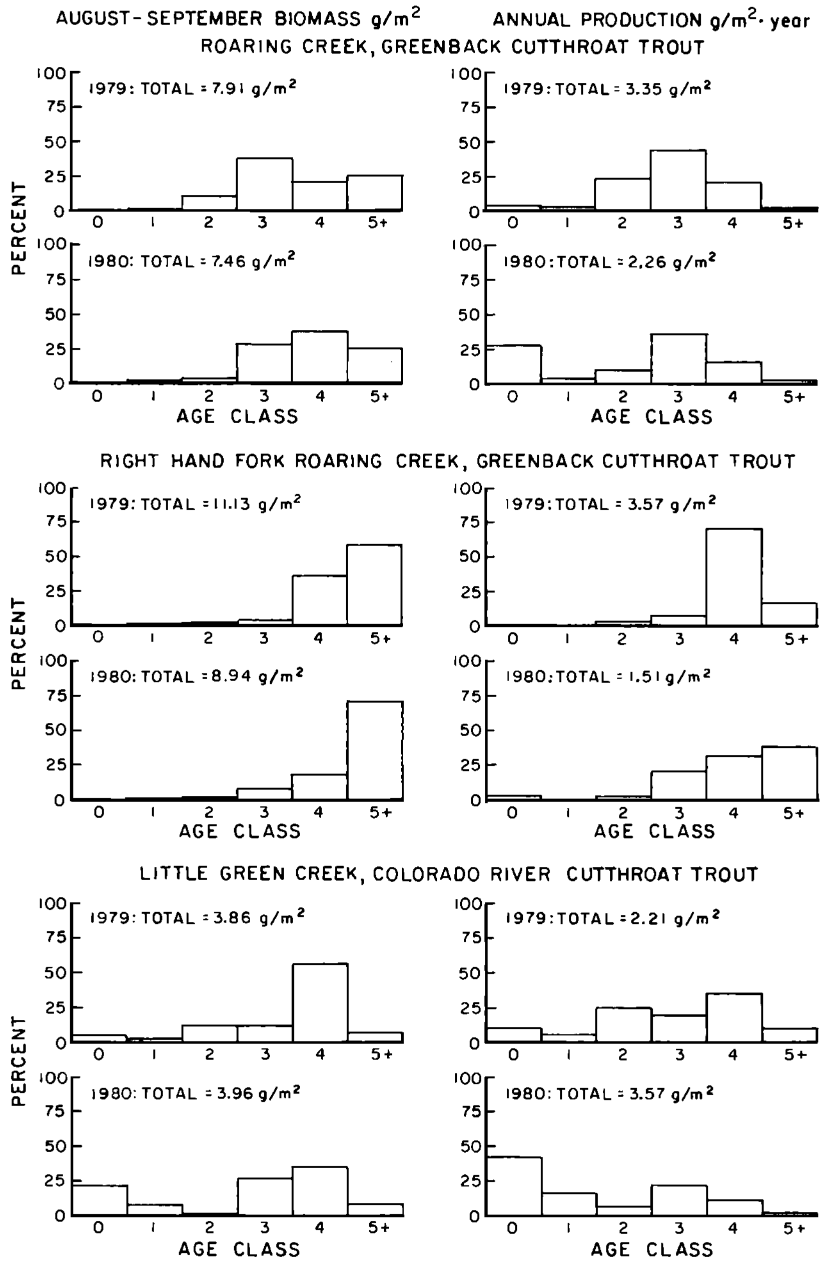

FIGURE 2.—Age distribution of August–September biomass and annual production of cutthroat trout in three Colorado streams, 1979 and 1980.

dominated by older fish (Figure 2). There were nine fish at least 152 mm long but fewer than two fish at least 202 mm long per 100 m^2 of stream. Although many young of the year were sampled in 1979, they contributed only 4% (0.15 g/m^2) of the total annual (January to December) production.

Production of young of the year increased in 1980 to 28% of the total (Figure 2). Production by the weak 1978 year class was low in both 1979 (1-year-old fish) and 1980 (2-year-olds). Year classes produced in both 1978 and 1979 were weak compared to those in 1977 and 1980.

Emergence of young of the year from the gravel

TABLE 2.—Average growth increments and instantaneous rates of daily growth (G)[a] of branded cutthroat trout recovered in three Colorado streams during 1979 and 1980.

Sampling interval	Number of fish recovered on both dates	Mean weight (g) Start	Mean weight (g) End	10^4G (day − 1)
Roaring Creek: greenback cutthroat trout				
Jul 31–Aug 1, 1979, to Sep 25–26, 1979	10	44.0	46.1	7.9
Sep 25–26, 1979 to Jul 9–10, 1980	6	50.0	51.0	0.7
Jul 9–10, 1980, to Aug 27–28, 1980	0			
Aug 27–28, 1980, to Oct 2–4, 1980	1	48.0	45.0	−17.9
Right Hand Fork Roaring Creek: greenback cutthroat trout				
Aug 2, 1979, to Sep 1–2, 1979	25	53.6	54.0	2.5
Sep 1–2, 1979, to Jul 11–12, 1980	11	43.5	49.0	3.8
Jul 11–12, 1980, to Aug 24, 1980	5	47.8	53.4	25.1
Aug 24, 1980, to Sep 30–Oct 1, 1980	6	70.7	66.2	−17.7
Little Green Creek: Colorado River cutthroat trout				
Aug 7, 1979, to Sep 16, 1979	13	44.4	44.5	0.6
Sep 16, 1979, to Jul 23, 1980	5	43.4	49.2	4.0
Jul 23, 1980, to Sep 11–12, 1980	4	42.0	44.8	12.9
Sep 11–12, 1980, to Oct 10–11, 1980	3	46.3	46.6	2.2

[a] $G = \log_e$(ending weight/starting weight)/days between samples.

apparently peaked near mid-August in both 1979 and 1980. Age-0 fish weighed an average 0.08 g on August 27, 1980 (Table 1). Individual fish reached 152 mm at age 3 or 4 and grew little thereafter. As judged by average weights for all age groups and by the few branded cutthroat trout recovered from Roaring Creek, growth rates were low during late summer (Table 2).

Right Hand Fork Roaring Creek.—Most of the production and biomass of greenback cutthroat trout in Right Fork were contributed by large fish aged 4 and older, even more so than in Roaring Creek (Figure 2). Young of the year and yearlings contributed negligible production.

Total production in 1980 dropped because of poor growth by larger fish, scant recruitment of young fish, and a scarcity of fish under 3 years old. Yearlings, which were not found as young of the year in 1979, were nearly absent in 1980—indicating a near failure of this year class in this section (Table 1). Biomass in 1980 consisted mostly of fish aged 4 and older.

In 1980, young-of-the-year fish apparently emerged from about August 15 until early September—later than in Roaring Creek (Table 1). On average, fish 152 mm long were at least 4 years old, and some were probably several years older. Growth of branded fish during August 1979 was slight (Table 2), but from September 1979 to July 11, 1980, 11 fish (average initial weight 43.5 g) gained an average of 5.5 g. Most of this growth apparently occurred during spring and early summer, because little or no growth occurred in autumn or winter.

Right Fork discharged about one-fifth as much water as Roaring Creek but supported a higher density of large cutthroat trout: 13 fish at least 152 mm long and slightly more than one fish over 202 mm long per 100 m^2.

Little Green Creek.—Production and biomass of Colorado River cutthroat trout in 1979 were dominated by fish 2 years old and older in Little Green Creek (Figure 2). Biomass during the August–September period was only about one-half that of Roaring Creek and one-third that of Right Fork. Young-of-the-year fish contributed only 5% of the total biomass.

Production in 1980 rose, mainly because production of young of the year rose to 1.5 g/m^2, or 43% of the total production (Figure 2). Twenty-two percent of the biomass consisted of young of the year.

In 1980, age-0 fish emerged from the gravel in late July to early August (Table 1), 2 to 3 weeks earlier than in Roaring Creek and Right Fork. Fish reached 152 mm at age 3 or 4. The greatest absolute gains in weight of branded fish were made from September 1979 to July 1980 (Table 2). Most of this growth apparently occurred in spring 1980, because there was little growth after August 1. One fish that weighed 37 g when branded on August 7, 1979, was recovered four times over the next 14 months; during this period it gained 13 g.

Of the three sections, Little Green Creek contained the lowest density of large fish: six fish per 100 m^2 at least 152 mm long and no fish as long as 202 mm.

Ratios of Production to Biomass

Production : biomass ratios in all three sections generally decreased with increasing age of fish (Table 3). Overall, ratios in Little Green Creek rose from 0.56 in 1979 to 0.79 in 1980 because pro-

TABLE 3.—Ratios of production to mean biomass for cutthroat trout in three Colorado streams, 1979 and 1980.

Age	Roaring Creek: greenback cutthroat trout		Right Hand Fork Roaring Creek: greenback cutthroat trout		Little Green Creek: Colorado River cutthroat trout	
	1979	1980	1979	1980	1979	1980
0	1.18	2.40		1.96	1.54	1.49
1	1.26	0.96	1.61	0.25	1.58	2.42
2	0.82	0.74	0.64	0.40	1.02	1.08
3	0.62	0.54	0.65	0.51	0.84	0.87
4	0.40	0.16	0.65	0.61	0.37	0.33
5 and older	0.03	0.03	0.11	0.12	0.06	0.06
All ages	0.47	0.33	0.35	0.23	0.56	0.79

duction of young of the year increased in 1980 and that of old, slow-growing fish decreased (Figure 2). In 1980, the ratios for Right Fork decreased because reproduction was poor and production of young of the year was scant. The ratios were higher in Roaring Creek than in Right Fork (where density of old fish was higher and that of young fish lower).

Habitat Features and Production

Physical differences between the three sections were associated with differences in production and biomass. Maximum summer temperature was 3°C higher in Little Green Creek than in Roaring Creek in 1979, and 5.5°C higher in 1980 (Table 4). Maximum temperatures in Roaring Creek were, in turn, higher than those in Right Fork (by 1.5°C in 1979 and 0.5°C in 1980). These differences in maximum temperatures were related to differences in time of emergence and production of young of the year. In both years, cutthroat trout in Little Green Creek emerged earliest and were the most productive (absolutely and by percentage), whereas those in Right Fork emerged latest and were the least productive. The 1979 year class continued in 1980 to be more productive in Little Green Creek than the same year classes in Roaring Creek or Right Fork (Figure 2). The comparatively warm water in Little Green Creek was associated with a lack of shading over most of the stream and a slow rate of flow (Table 4).

Diversity of substrates was lower in Little Green Creek than in Roaring Creek and Right Fork (Table 4). The substrate in Little Green Creek was about 85% fine and coarse gravel (Figure 3); less than 5% consisted of combined cobble and boulder, compared with over 20% in Roaring Creek and over 40% in Right Fork. At many stations in

TABLE 4.—Physical attributes of three Colorado streams, 1979 and 1980.

Variable	Year	Roaring Creek	Right Hand Fork Roaring Creek	Little Green Creek
Maximum temperature (°C)	1979	15.5	14.0	18.5
	1980	15.5	15.0	21.0
Mean depth (cm)	1979	17	10	13
	1980	15	11	13
Mean velocity (m/s)	1979	0.15	0.11	0.05
	1980	0.16	0.12	0.03
Substrate diversity[a]	1979	0.60	0.61	0.35
	1980	0.68	0.71	0.52
Mean width/mean depth	1979	18	14	12
	1980	22	15	11
Undercut banks (cm/m of stream)	1979	6	13	10
	1980	7	19	13
Percentage of 0-velocity stations	1979	46	56	77
	1980	46	60	79
Conductivity (μS/cm at 25°C)	1979	38	36	77
	1980	33	31	62

[a] Shannon–Weiner index = $\sum_{i=1}^{s} (P_i)(\log_2 P_i)$; s = number of substrate classes; P_i = proportion of the total sample belonging to the ith class.

Little Green Creek, it was difficult to detect any flow. These increasing percentages of gravel and decreasing velocities from Right Fork to Little Green Creek (Table 4, Figure 3) corresponded to increasing biomass and production of young of the year (Figure 2).

The extent of cover provided by undercut banks was positively related to the biomass of large fish among the sections. Right Fork had the greatest extent of undercut banks of the three streams in both 1979 and 1980, and was deeper for its width than Roaring Creek. Roaring Creek also had only about 70% as many large fish (at least 152 mm long) per unit area as did Right Fork. The greater amount of cover provided by the undercut banks of Right Fork thus coincided with the higher density of large trout.

None of the streams were chemically fertile; all conductivities were below 80 μS/cm (Table 4). Within this limited scope, conductivity was unrelated to annual production of cutthroat trout among the three study sections.

Water contents of snowpacks at the Deadman Hill and Columbine sites were above average in both 1979 and 1980. In these years, the production of young-of-the-year fish was less than 4% of the total in Right Hand Fork (Figure 2) but, in Roaring Creek and Little Green Creek, production in 1980

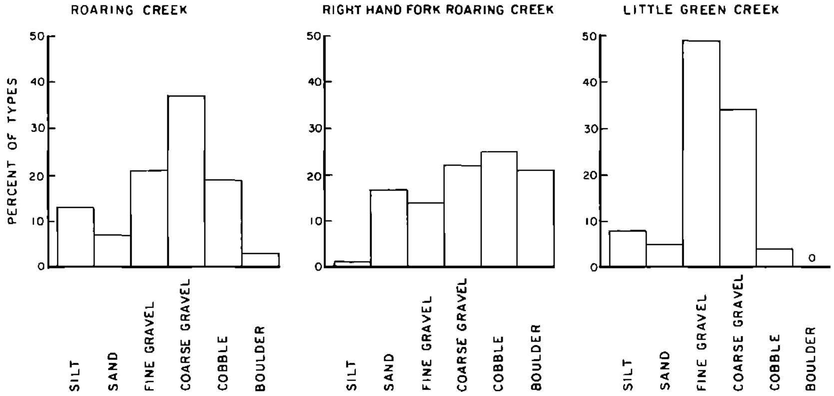

FIGURE 3.—Percentage composition of substrates in Roaring Creek, Right Fork, and Little Green Creek in 1980. No plant detritus or clay was detected in any samples.

rose to 29% and 43%, respectively, of total production in these streams, despite the high snowpack. The abnormally low snowpack in 1977 did not appear to coincide with unusually strong year classes of age-2 fish in 1979 or age-3 fish in 1980 in any of the streams.

Discussion

The production of cutthroat trout in Little Green Creek, Roaring Creek, and Right Fork varied from 1.5 to 3.6 g/m^2, which is low compared with that reported for salmonids in most rivers studied (Le Cren 1969; Chapman 1978; Mortensen 1979). Overall ratios of production to biomass, which ranged from 0.23 to 0.79, were also lower than ratios for resident brook trout in Quebec (0.70–1.65: O'Conner and Power 1976), anadromous and resident brown trout in Denmark (0.7–1.8: Mortensen 1977), or brown trout in the United Kingdom (1.5–3.0: data from Mann 1971; production calculated by Chapman 1978). The low production in our study streams probably results from the late emergence and subsequent scarcity of young cutthroat trout and the slow growth of large fish, among which angling and natural mortality are low. These biological factors are related, in turn, to the cold winters and short growing seasons at high elevations in northern Colorado. Chapman (1978) noted that production : biomass ratios usually are in the range 0.9–2.4, but that production and ratios may be lower in cold streams. Crisp et al. (1975) found lower production of brown trout in high-elevation headwater sections of the River Tees than in most English lowland streams. The low production in the present three streams is consistent with these investigations.

The three streams differed markedly from each other in relative biomass and production of young of the year, which were both highest in Little Green Creek where fine gravel and slow flows were most prevalent. Rinne (1980) reported that Gila trout *Salmo gilae* spawned preferentially in gravel 0.2–3.8 cm in diameter, which corresponds to the fine gravel and lower half of the coarse-gravel categories in the modified Wentworth scale we used. Harper (1978) showed that Apache trout *S. apache* generally selected gravel 0.085–3.2 cm in diameter for spawning—again in the fine- and coarse-gravel categories. We observed no spawning by either subspecies of cutthroat trout. However, if the Colorado River and greenback cutthroat trouts have preferences similar to those of Gila and Apache trouts, then the section of Little Green Creek has abundant spawning gravel, Roaring Creek has a moderate amount, and Right Fork has little. Little Green Creek also had the slowest-moving water, which is suitable for rearing small trout after they have emerged from the gravel. For Right Fork, however, the abundance of large trout in the study section, the scarcity of spawning gravel, the presence of fast flows, and our observation of ample spawning gravel 200 m above the study section may indicate that many of the large fish colonized this section from upstream or downstream reaches. Such a colonization would explain the scarcity of fish less than 3 years old. Bulkley (1959) suggested that greenback cutthroat trout, like Gila trout (Rinne 1982), are sedentary, but abundant spawning gravel in the stream we studied may have obviated the need for migrations.

Because the cutthroat trout emerged late (August–September) in all three creeks, and especially in Right Fork, few exceeded lengths of 30–35 mm before winter. Emergence in Right Fork, where young of the year were scarcest, was later than for similar species of *Salmo* in more southerly waters. Harper (1978) reported that Apache trout emerged mainly from August 1 to 15 in Big Bonito Creek, Arizona; Rinne (1980) observed young-of-the-year Gila trout as early as June 25 in New Mexico. Although genetic differences between the species undoubtedly exist, key physical environmental factors such as water temperatures may result in life history differences between these species. Eggs may be deposited later and develop more slowly in Colorado streams such as Roaring Creek and Right Fork than in New Mexico and Arizona because water temperatures are lower. If so, in years of above-average snowpacks such as 1979 and 1980, spring runoff would be protracted, spawning and emergence would be later, and year classes may be weaker. Drummond (1966) showed that annual recruitment of age-0 fish from Cabin Creek into Trapper's Lake, Colorado, was inversely related to water content of the snowpack in that winter (over the normal range of snowpacks), and directly related to eventual success of anglers in catching adult fish of this age group. Nehring and Anderson (1983) subsequently found that the strength of year classes of brown trout in the South Fork of the Rio Grande was inversely related to snowpack levels and summer rains.

Although our data were limited, abundance and production of young of the year were high in 1980 in Roaring Creek and Little Green Creek (Figure 2), despite high snowmelt. However, heavy summer rains may have depressed water temperatures and reduced year-class strengths in 1979, as Nehring and Anderson (1983) concluded for the South Fork of the Rio Grande. We observed that the summer was much drier in 1980 than in 1979 in the vicinity of all three streams—as reflected by the high maximum temperatures in Right Fork and Little Green Creek in 1980 (Table 4). Survival and production of young of the year were also higher in Roaring Creek and Little Green Creek in 1980 than in 1979. We also believe that year-class strength in these streams was depressed by high abundances of large trout in the sections. For example, a 63% reduction in biomass of fish of age 4 and older in Little Green Creek in 1980 corresponded to a sixfold increase in production of young of the year. Reductions in cannibalism, crowding, or both, may have led to this increased production of young fish. Rinne (1980) observed cannibalism on small Gila trout by larger ones, but Bulkley (1959) found that greenback cutthroat trout ate aquatic and terrestrial invertebrates, not fish. Although more thorough feeding studies are needed on greenback and Colorado River cutthroat trout in small streams, Bulkley (1959) concluded that much of the mortality of age-0 fish must result from factors other than predation.

We believe that crowding is a main cause of this mortality of age-0 fish. In late summer, when the young of the year emerge, streamflows are low and habitat is scarce. The reduction in the number of older fish in Little Green Creek in 1980 reduced intraspecific crowding, which in turn led to increased overall production and a higher turnover ratio, and may have allowed higher survival of age-0 fish. The depressing effects of older fish on production may be more severe in small streams, where fish of all ages are closer together, than in larger streams (Nehring and Anderson 1983) and streamfed lakes (Drummond 1966), where more segregation of the age groups is likely.

Although genetic differences between the stocks undoubtedly exist, physical factors also exert a strong influence on production and biomass of cutthroat trout in these three stream sections. In addition, at least three other biological factors affect the abundance and production of young-of-the-year cutthroat trout: the time of emergence of juveniles; growth rates of juveniles prior to their first winter; and the abundance of large resident adult fish.

Acknowledgments

A National Wildlife Federation fellowship and a Sport Fishing Institute research grant provided additional valuable support for this research. We thank S. Horak and M. Giossi for field assistance. We also thank R. B. Nehring, R. F. Raleigh, R. J. Behnke, and anonymous reviewers for commenting on the manuscript.

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Received February 6, 1985
Accepted April 21, 1986