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Trout Production and Standing Crop in Colorado's Small Streams, As Related to Environmental Features

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Abstract.—Annual production of trout (*Salvelinus* and *Salmo* spp.) in 10 small northern Colorado streams (elevation 2,146–3,139 m above sea level) ranged from 1.5 to 18.4 g/m^2 in 1979 and 1980. Midsummer biomass ranged from 3.9 to 28.2 g/m^2. Ratios of production to biomass ranged from 0.23 to 0.95. Fish production and biomass were related inversely to elevation and directly to substrate diversity, conductivity, alkalinity, and water hardness. Combinations of the various factors explained much of the variation in production: elevation and width : depth ratio, 60%; elevation and substrate diversity, 54%; elevation, substrate diversity, and percentage of zero-water-velocity stations, 79%; and elevation, width : depth ratio, and alkalinity, 77%. Similar relationships were developed for midsummer biomass. There was a strong correlation between midsummer biomass and annual production as well as between annual production and the density of fish of desirable size (152 mm long or longer) in each stream. Several relationships are proposed from these data sets that can be used to predict trout production in small, high-elevation streams. Estimated habitat quality indices for the 11 sections were significantly related to midsummer biomass of trout in 1979 but not in 1980.

The production of salmonids in streams has been studied frequently over the past 30 years (Allen 1951; Chapman 1979; Mortensen 1979). Although many researchers have quantified physical and chemical characteristics of streams in which they also measured production (Chapman 1965; Hunt 1966; Le Cren 1969; Egglishaw and Shackley 1977; Mortensen 1977), few have attempted to systematically relate combinations of these physical and chemical characteristics to the observed production. Consequently, few of these studies have resulted in the development of models of salmonid production.

Power (1973) explained variations in production of Arctic char *Salvelinus alpinus*, brown trout *Salmo trutta*, and Atlantic salmon *Salmo salar* in northern Norwegian rivers by the sediment composition of stream bottoms, width of streams, presence or absence of glacial silt, and land-use characteristics of the river valleys. Le Cren (1969) showed that production was much higher in English streams high in calcium than in those low in calcium, even though most extra production was contributed by nonsalmonids. Most other habitat models for salmonids have been developed for evaluating biomass (standing crop) rather than production. Binns and Eiserman (1979) developed a "habitat quality index" (HQI) based on nine

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physical, chemical, and biological attributes that explained 90% of the variation in biomass of salmonids in Wyoming streams. Burton and Wesche (1974), who related standing crops of salmonids in 11 Wyoming streams to 18 different watershed variables, found that standing crop was inversely related to total stream length, drainage area, and stream order, and directly related to storage capacity, mean and median basin elevation, and amount of forest cover. The U.S. Fish and Wildlife Service has developed "habitat suitability index" models for riverine salmonids based mainly on physical factors at four life stages—adult, juvenile, fry, and embryo (Hickman and Raleigh 1982; Raleigh 1982).

It is too expensive and time consuming to measure production in even a small percentage of Colorado's small streams. For small (first- to third-order) streams, it may also be impractical to monitor such factors as daily variation in water temperature or to quantify intricate physical factors such as cover. A more realistic approach would be to develop simple relationships to predict production and standing crop. Such an approach was pursued by Binns and Eiserman (1979), whose model II predicted standing crops on the basis of nine easily measured physical and chemical factors.

The main objective of our study was to develop simple empirical relationships for predicting trout production in Colorado's small, permanently flowing streams on the basis of easily measured physical and chemical attributes. Our secondary objective was to test how well Binns and Eiserman's (1979) HQI model II predicted standing crops in Colorado trout streams.

Study Sites

The 10 streams studied are in northern Colorado (Figure 1); all are perennial, contain trout populations consisting of several age-groups, are small enough for reliable population estimates, and are either lightly fished or unfished. Elevations range from 2,146 to 3,139 m above mean sea level (Table 1). Two sections of Dale Creek (Dale 1 and Dale 2) and one section of each of the other nine streams were sampled. Seven of the sections were 200 m long; the other four were 100–190 m long. The canopies varied from dense spruces and firs over Davis Creek to open meadow surrounding Little Green Creek (Scarnecchia 1983). One of four species of trout—brook trout *Salvelinus fontinalis*, cutthroat trout *Salmo clarki*, rainbow trout *Salmo gairdneri*, or brown trout—dominated each stream except in Dale and Cow creeks, where two species were well represented (Table 1). The stream sections were described in detail by Scarnecchia (1983).

Methods

Population estimates.—We sampled fish with backpack electrofishing units in each section twice in 1979 and three times in 1980 (Table 1). Nunn Creek was sampled three times each year. Before electrofishing, each section was blocked at its upper and lower ends with fine-mesh seines. Captured fish were retained temporarily in baskets placed in the stream at intervals along each section (Scarnecchia 1980). After recording lengths and weights for all fish except young of the year (which we subsampled), we returned each fish, when possible, to the pool or riffle from which it had been removed. Sampling efficiency was high, generally 95 to 100% of the estimated populations (Table 2). Populations were estimated by the three-pass removal method (Zippin 1956, 1958) from the Y intercept of an X on Y regression of catch in the ith trapping (X) on previous total catch (Y). Populations were estimated separately by age when sample sizes were large enough, but more often the fish of different ages were grouped. The total population estimate was then partitioned back into separate ages on the basis of the number of fish of each age caught. For each section, the densities of fish 152 mm long and longer and of 202 mm and longer were calculated from the average of the population estimates and expressed as the numbers of fish of at least those lengths per unit of surface area.

Snowstorms in 1980 prevented the sampling of more than the lower 100 m of the study section in Porcupine Creek on October 15, and all of Dale 1 and two-thirds of Dale 2 on November 10. Populations in these sections were estimated for these dates by assuming that the ratio of the estimated population sizes for the sampled portion of the streams to estimates for the complete sections did not change between previous complete sampling and later incomplete sampling.

Age determination.—Ages were determined mainly by length-frequency distributions and scale reading. In general, both methods proved effective for fish up to 4 years old. Otoliths and pectoral fin rays also were used selectively to confirm the accuracy of age determinations. During the last population surveys of 1980, small samples of otoliths obtained from brook trout in Porcupine Creek and from cutthroat trout in Roaring Creek were inter-

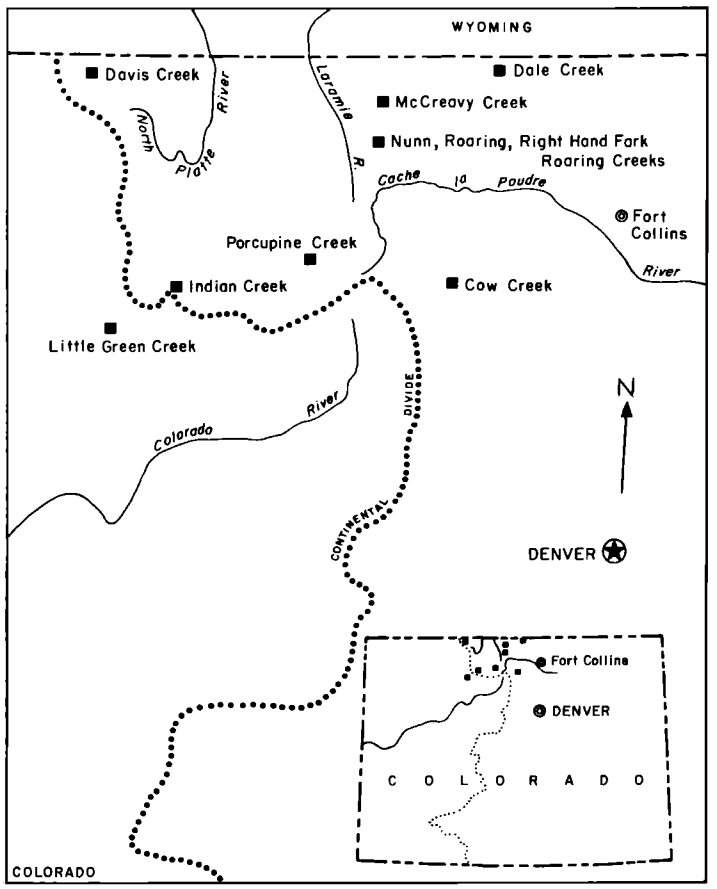


FIGURE 1.—Locations of 10 Colorado streams in which production of trout was investigated.

preted according to methods outlined by Williams and Bedford (1974). Pectoral fin rays also were collected from a few brown trout from Nunn Creek. They were clipped close to the point of attachment and mounted in trays filled with liquid plastic. After the plastic was solidified with a catalyst, thin cross sections of each ray were sliced and aged under a microscope according to methods described by Bilton and Jenkinson (1969), Burnet (1969), and Shirvell (1981). Fin rays and otoliths proved reliable for cross-checking ages, but scales, fin rays, and otoliths were difficult to interpret from slow-growing fish of all species older than 4 or 5 years. For Roaring Creek, Right Fork of Roaring Creek (henceforth termed Right Fork), and Porcupine Creek (less so for the other streams), the oldest age-group identified probably included fish several years older than 4 or 5 years.

During the first population estimates for 8 of the 11 sections, some fish longer than 135 mm were branded with silver tipped branding irons (Groves and Novotny 1965). We used a coded system based on binary numbers to enable us to identify recaptured fish. During the second samplings of the streams, some previously unbranded fish were branded. Branded fish recovered were identified, weighed, and measured during the second and subsequent three samplings.

Production estimates.—Annual production P, in grams per square meter, was calculated for each age-class and stream as $P = G\bar{B}$ (Ricker 1946); G is instantaneous growth rate and $\bar{B}$ is the average biomass over an interval t for which G is constant. Values for $\bar{B}$ were calculated as

$$\bar{B} = \frac{B_0(e^{G-Z} - 1)}{G - Z}$$

(Ricker 1975). Annual average biomass for each stream each year was computed as the arithmetic average of $\bar{B}$ values between sampling intervals.

Trout population sizes ($\hat{N}$) and average weights

TABLE 1.—Sampling dates and characteristics of 11 study sites in which trout production was investigated in 1979 and 1980. Sites were 100–200 m long.

Creek	Sampling dates 1979	Sampling dates 1980	Stream order	Characteristics of study section: Elevation above sea level (m)	Mid-summer discharge[a] (m^3/s)	Width in mid-summer[a] (m)	Fish species present
Dale 1	Jun 19–21 Oct 10–12	Jun 24–25 Aug 5–7 Nov 10	3	2,146	0.14	3.6	Brook trout Rainbow trout Brown trout[b] Longnose sucker[b,c]
Dale 2	Jun 24–26 Oct 16–18	Jun 26–29 Aug 8–11 Nov 10	3	2,146	0.14	4.7	Brook trout Rainbow trout Brown trout Longnose sucker[b]
McCreavy	Jul 14 Aug 23–24	Jul 1 Aug 20–21 Sep 26–27	1	2,542	0.003	0.6	Brook trout Brown trout[b]
Nunn	Jul 19 Aug 28 Oct 25–26	Jul 8 Aug 22–23 Sep 24–25	2	2,938	0.019	1.9	Brown trout Cutthroat trout[b]
Roaring	Jul 31–Aug 1 Sep 25–26	Jul 9–10 Aug 27–28 Oct 2–4	2	2,987	0.074	3.1	Cutthroat trout
Right Fork[d]	Aug 2 Sep 1–2	Jul 11–12 Aug 24 Sep 30	1	3,139	0.019	1.6	Cutthroat trout
Indian	Aug 9 Sep 18	Jul 24–25 Sep 13–14 Oct 12–13	2	2,716	0.012	2.2	Brook trout Longnose sucker
Little Green	Aug 7 Sep 16	Jul 23 Sep 11–12 Oct 10–11	2	2,807	0.009	1.5	Cutthroat trout
Davis	Aug 14 Oct 3	Jul 27–28 Sep 17–18 Oct 13–14	2	2,835	0.044	4.0	Brook trout Brown trout[b]
Porcupine	Aug 21–22 Oct 4–5	Jul 29–30 Sep 19–20 Oct 15	1	3,066	0.023	1.5	Brook trout
Cow	Jul 25–26 Sep 10–11	Jul 16–18 Sep 4–6 Oct 21–23	1	2,469	0.037	3.2	Brook trout Brown trout

[a] Values for discharge and width were derived from the arithmetic average of one 1979 and one 1980 measurement between August 1 and October 30 each year.
[b] Species rarely found.
[c] *Catostomus catostomus*.
[d] Right Hand Fork of Roaring Creek.

($\bar{W}$) by age were estimated satisfactorily during summer and early fall, but not during winter or during periods of high runoff in the spring. For example, weight data (Scarnecchia 1983) indicated that fish grew rapidly during the spring; consequently we needed to estimate production for this period. To do so, we assumed that fish did not grow between November 1 and April 30 (for all streams except Dale Creek) or from November 16 to March 31 in Dale Creek. Overwinter mortality rates for fish of all age-groups were assumed to be exponential. In both 1979 and 1980, population sizes and average weights were estimated inferentially for November 15 and April 1 for Dale Creek, and for October 31 and May 1 for the other streams. These estimates were based on assumptions of steady state mortality and on yearly growth and mortality trends.

The ages of brook trout could not be reliably determined beyond age 3 in Davis Creek and age 4 in Porcupine Creek. The ages of cutthroat trout could not be accurately determined beyond age 4

TABLE 2.—Average electrofishing trout catches as a percentage of total population estimates of age-groups 0 and older for 10 Colorado streams, 1979 and 1980.

	Age-group					
	0		1 and older		Combined	
Creek	Range	Average	Range	Average	Range	Average
Dale 1	77–90	83	93	93	66–96	89
Dale 2	85	85	99	99	89–95	92
McCreavy	85–100	94	94–100	98		
Nunn					91–100	96
Roaring	79–88	83	94–100	98		
Right Fork	76–100	88	100	100	100	100
Indian	93–100	95	95–100	98		
Little Green	77–100	87	87–100	97		
Davis	80–100	95	95–100	97		
Porcupine	63–91	82	94–99	98	96	96
Cow	97–100	94	93–100	98		

in either Roaring Creek or Right Fork. For older fish in these streams, we assumed that annual growth in grams was equal to that of branded fish of comparable size in each stream.

Habitat measurements.—Fourteen physical and chemical characteristics for each section were measured or calculated once in 1979 and once in 1980 between August 1 and October 31 (Tables 1, 3, and 4). 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 upstream end of the section. Seven equidistant stations were established along each transect, the fourth of which was in the center of the stream; thus there were 11 transects and 77 stations in a section 200 m long and 6 transects and 42 stations in a section 100 m long (Stewart 1970).

We measured the width of the stream at each transect. At each station, the depth was recorded and the substrate was evaluated visually by particle size according to a modified Wentworth classification. An average width : depth ratio was calculated. Substrate diversity was estimated later by applying the Shannon–Weiner index (Pielou 1975). Velocity was measured at 0.6 of the depth (Stalnaker and Arnette 1976) with an Ott model C2 current meter. Mean velocity, the percentage of zero-velocity stations, and discharge also were determined. Canopy was visually ranked from 1 to 5 (1 = open meadow; 5 = dense forest).

We determined the number of undercut banks by measuring the along-stream length of any section of stream 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 expressed as centimeters of undercut bank per meter of stream.

The maximum summer temperature of the water

TABLE 3.—Physical attributes of 10 small streams in northern Colorado, 1979 and 1980.

	Maximum temperature (°C)		Mean depth (cm)		Mean velocity (m/s)		Substrate diversity		Mean width : mean depth		Undercut banks (cm/m of stream)		Percent of 0-velocity stations	
Creek	1979	1980	1979	1980	1979	1980	1979	1980	1979	1980	1979	1980	1979	1980
Dale 1	[a]	18.5	18.7	20.3	0.146	0.228	0.70	0.74	18.1	18.8	5.2	11.8	41	24
Dale 2	[a]	18.5	14.3	16.3	0.167	0.235	0.65	0.63	31.3	29.6	6.3	12.8	38	22
McCreavy	15.0	17.0	9.1	9.0	0.080	0.023	0.77	0.73	6.7	6.7	10.1	9.7	68	89
Nunn	21.5	22.0	16.9	19.0	0.044	0.064	0.39	0.49	11.5	10.1	6.4	7.9	77	77
Roaring	15.5	15.5	16.9	14.6	0.148	0.162	0.60	0.68	17.9	22.4	6.4	7.1	46	46
Right Fork	14.0	15.0	10.1	11.4	0.109	0.121	0.61	0.71	14.4	14.5	12.5	18.9	56	60
Indian	20.0	23.0	12.6	13.6	0.029	0.053	0.56	0.52	15.8	17.6	11.8	13.4	86	77
Little Green	18.5	21.0	13.3	13.6	0.053	0.033	0.35	0.52	11.5	11.1	10.2	13.1	77	79
Davis	10.5	13.0	11.5	11.5	0.106	0.087	0.45	0.45	35.1	34.4	15.7	18.5	57	62
Porcupine	14.5	17.0	15.0	14.6	0.142	0.068	0.69	0.59	10.1	9.7	16.5	17.1	69	77
Cow	14.5	16.0	7.7	8.2	0.156	0.136	0.73	0.69	44.3	35.4	18.3	18.7	46	53

[a] Value for 1980 used in regression analyses.

TABLE 4.—Chemical attributes of 10 small streams in northern Colorado, 1979 and 1980.

Creek	Alkalinity (mg/L)		Total hardness (mg/L)		Conductivity (μS)		Nitrates (μg/L)	
	1979	1980	1979	1980	1979	1980	1979	1980
Dale 1	119.7	116.3	102.6	111.2	193.9	219.2	82.2	54.0[a]
Dale 2	95.8	116.3	102.6	119.7	232.8	232.8	82.8	54.0[a]
McCreavy	61.6	55.6	68.4	51.3	118.1	98.6	17.0	3.2
Nunn	47.9	42.8	51.3	34.2	83.1	73.4	26.4	3.2
Roaring	27.4	21.4	17.1	12.8	38.4	32.5	20.5	21.5
Right Fork	20.5	17.1	17.1	12.8	36.4	30.6	69.0	71.0
Indian	102.6	68.4	68.4	64.1	129.7	129.7	25.0	10.0
Little Green	68.4	42.8	51.3	34.2	77.3	61.7	51.0	10.0
Davis	41.0	34.2	51.3	25.7	65.6	59.8	61.0	16.0
Porcupine	34.2	29.9	34.2	29.9	55.9	53.9	36.0	16.0
Cow	34.2	17.1	17.1	12.8	46.1	34.5	42.0	16.0

[a] Measured June 30, 1980; all other variables were measured in midsummer.

was determined in each section with a maximum–minimum thermometer that was left in place between successive samplings. Conductivity was measured with a Beckman RB 3 Solubridge calibrated with potassium chloride standard solutions (APHA et al. 1975). Alkalinity was measured with a Hach model AL-AP test kit and total hardness with a Hach model HA-4P test kit. Nitrates were measured by the cadmium-reduction method with a Perkin–Elmer spectrophotometer.

Habitat quality indices.—Application of Binns and Eiserman's (1979) HQI model II required the measurement or classification of nine habitat attributes: late-summer streamflow (X_1), annual streamflow variation (X_2), maximum summer stream temperature (X_3), nitrates (X_4), percent cover (X_7), eroding banks (X_8), substrates and submerged aquatic vegetation (X_9), water velocity (X_{10}), and stream width (X_{11}). (Variables X_5 and X_6 relate to the abundance and diversity of fish food, which Binns and Eiserman used in their model I but not in model II.) Binns and Eiserman rated each measured estimate of an attribute with an integer from 0 (worst) to 4 (best). For some attributes (e.g., percent cover, X_7), the higher the measured value, the higher (better) the rating. For other attributes (e.g., maximum summer stream temperature), ratings at intermediate measurements were best, and extremely high and low measurements rated poorly. (See Table 3 of Binns and Eiserman 1979.) Their relationship between standing crop (Y) and the nine habitat variables was

$$\log_{10}(Y + 1) = [(-0.903) + (0.807)\log_{10}(X_1 + 1) + (0.877)\log_{10}(X_2 + 1) + (1.233)\log_{10}(X_3 + 1) + (0.631)\log_{10}(F + 1) + (0.182)\log_{10}(S + 1)][1.12085];$$

F = food index = $(X_3)\cdot(X_4)\cdot(X_9)\cdot(X_{10})$;
S = shelter index = $(X_7)\cdot(X_8)\cdot(X_{11})$.

The factor of 1.12085 was used to convert pounds per acre to kilograms per hectare.

Three measurements for our production models (width, maximum summer stream temperature, and nitrates) were the same as those required for the HQI. For the HQI estimates of water velocity, Binns and Eiserman (1979) divided thalweg length by the time required for a fluorescent dye to travel through that section. We converted our transect velocity measurements to their measurement by assuming that the average of our maximum measured velocities at each transect would indicate, at least approximately, the rate at which dye would traverse a stream section. Estimates were then rated on their scale to classify velocities for each stream.

The other five attributes (late-summer streamflow, annual streamflow variation, cover, eroding banks, and substrate) were not directly measured in our streams. There were no gauging stations on any of the streams, and ratings for late-summer streamflow and annual streamflow variation were estimated from channel morphology and observations of flows during late spring, summer, and fall. Most streams were easily classified because of large differences between HQI rating characteristics and the absence of poor trout streams in our study; all rated 3 or 4 for late-summer flows and 2 or 3 for annual streamflow variation. Each stream had moderate to small fluctuations in annual flows and at least adequate summer flows. Ratings for eroding banks were based on detailed photographs and observations of each stream section. (All reaches of each section had been photographed in sequence as part of the production study.) Substrates (as percent of submerged aquatic vegeta-

TABLE 5.—Annual production and midsummer biomass of trout and their rankings (1–11) for 10 small streams in northern Colorado, 1979 and 1980.

Creek	Production, 1979		Biomass, 1979		Production, 1980		Biomass, 1980	
	g/m²	Rank	g/m²	Rank	g/m²	Rank	g/m²	Rank
Dale 1	10.6	2	28.2	1	8.8	2	20.1	2
Dale 2	9.6	3	20.3	2	7.5	4	14.3	4
McCreavy	12.6	1	14.1	3	18.4	1	26.3	1
Nunn	5.2	5	13.3	4	3.4	8	10.1	6
Roaring	3.3	9	7.9	9	2.3	9	7.5	8
Right Fork	3.6	8	11.1	6	1.5	11	8.9	7
Indian	5.2	5	9.3	8	4.4	6	7.1	9
Little Green	2.2	10	3.9	11	3.6	7	4.0	11
Davis	1.7	11	4.4	10	1.9	10	5.9	10
Porcupine	4.8	7	10.4	7	4.9	5	10.6	5
Cow	6.3	4	13.2	5	8.3	3	17.6	3

tion) were estimated from observations, field notes, and substrate data from the production study.

Cover was the most subjective of the measurements rated. Our cover measurements for this production study consisted of only the measurement of undercut banks. However, Binns and Eiserman (1979) correctly identified cover as consisting of "water depth, surface turbulence, loose substrate, large rocks and other submerged obstructions, undercut banks, aquatic and overhanging terrestrial vegetation, dead snags and other debris lodged in the channel, and anything else that allows trout to avoid the impact of the elements or enemies." Cover in the HQI was expressed as percent cover in each section. Cover ratings for our streams were based on our measurement of undercut banks, detailed photographs of the stream sections, field notes, and personal experience with the streams. The senior author had walked along and in each stream section at least 15 times over a 2-year period while electrofishing.

After ratings had been established for each stream, none were changed nor were any exploratory HQI calculations made. We calculated HQI values once for each stream (as described later) using the HQI expression and the data in Tables 1, 3, and 4.

Statistical analyses.—Relationships between production, biomass, physical and chemical factors, and HQIs were investigated by using simple, multiple, and stepwise regressions and analysis of variance techniques (Snedecor and Cochran 1967; Neter and Wasserman 1974; Nie et al. 1975). In most analyses, data for 1979 and 1980 were combined ($N = 22$). Although Binns and Eiserman (1979) assumed dome-shaped relations between some habitat attributes and their suitability as trout habitat, our preliminary plots of individual physical and chemical factors against production and biomass showed no apparent dome-shaped relationships over the ranges of our observed values. Consequently, we used linear equations for analyses of these streams.

Results

Production and Biomass

Annual production in the 11 sections ranged from 1.5 g/m² in Right Fork in 1980 to 18.4 g/m² in McCreavy Creek in 1980 (Table 5). Production rankings among the streams changed little between 1979 and 1980 (Spearman rank correlation $r^2 = 0.71$; $P < 0.01$). However, production in McCreavy Creek rose by 5.8 g/m² in 1980 over 1979 because of the large production of young of the year in 1980. Midsummer biomass in the 11 sections ranged from 3.9 g/m² in Little Green Creek in 1979 to 28.2 g/m² in Dale 1 in 1979. Like the production rankings, biomass rankings among the streams were similar in 1979 and 1980 (Spearman rank correlation $r^2 = 0.79$; $P < 0.01$). Biomasses of age-groups differed greatly among streams.

There were large contributions to total biomass by brook trout of ages 0 and 1 in McCreavy Creek in both years and in Indian Creek in 1980, but scant or no contributions by these age-groups of brown trout in Nunn Creek in either year. Because the streams were unfished or lightly fished, high percentages of the biomasses in most streams represented large, sexually mature fish (Scarnecchia 1983).

Ratios of production to biomass ($P{:}\bar{B}$) ranged from 0.23 for Right Fork, dominated by large cutthroat trout, to 0.95 for McCreavy Creek, which contained many young-of-the-year brook trout (Table 6). The $P{:}\bar{B}$ ratios, in part, indicated pop-

TABLE 6.—Annual ratios of production (g/m^2) to mean biomass (g/m^2) for trout populations in 10 small streams in northern Colorado, 1979 and 1980.

Creek	Trout species	Ratio 1979	Ratio 1980
Dale 1	Brook, rainbow	0.56	0.50
Dale 2	Brook, rainbow	0.55	0.53
McCreavy	Brook	0.95	0.90
Nunn	Brown	0.41	0.34
Roaring	Cutthroat	0.47	0.33
Right Fork	Cutthroat	0.35	0.23
Indian	Brook	0.74	0.79
Little Green	Cutthroat	0.56	0.79
Davis	Brook	0.43	0.37
Porcupine	Brook	0.49	0.53
Cow	Brook, brown	0.68	0.52

ulation age and size structure; those ratios in Little Green Creek rose from 0.56 in 1979 to 0.79 in 1980 coincident with a decrease in biomass of the large and older fish (Scarnecchia and Bergersen 1986).

Dale 1 had the highest density of trout at least 152 mm long (24 fish/100 m^2) and at least 202 mm long (10.4 fish/100 m^2). Densities of larger fish in other streams were as low as six 152+-mm fish (Davis Creek) and no 202+-mm fish per 100 m^2 (Little Green and Porcupine creeks) (Table 7).

Age Structure Relationships

The age structure of the populations in several of the streams also was related to the composition of the substrate. In Little Green Creek, where the substrate was mostly fine and coarse gravel, many young-of-the-year cutthroat trout, but few as long as 152 mm, were collected in both years. In Right Fork, where cobble and boulders were more common than in Roaring Creek, the density of large cutthroat trout also was higher (Scarnecchia and Bergersen 1986). Both gravel substrate and production of young-of-the-year cutthroat trout were higher in Roaring Creek than in Right Fork. In Cow and Porcupine creeks, whose banks were not grazed and where the substrate was diverse, each age-group of brook trout was well represented. In contrast, Davis Creek, where the substrate consisted of mostly large cobble and boulder and included little spawning gravel, had low production and low biomass (Scarnecchia 1983).

TABLE 7.—Densities of large trout (number/100 m^2) in 10 small streams in northern Colorado, 1979 and 1980 combined.

Creek and trout species	Total length (mm) ≥202	Total length (mm) ≥152
Dale 1[a]		
Brook	4.9	10.8
Rainbow	4.7	12.2
Brown	0.8	0.8
Total	10.4	23.8
Dale 2[a]		
Brook	4.9	10.8
Rainbow	3.1	7.3
Brown	0.1	0.1
Total	8.1	18.2
McCreavy		
Brook	0.8	13.2
Brown	2.4	2.0
Total	3.2	15.2
Nunn		
Brown	6.0	15.4
Cutthroat	<0.1	0.2
Total	6.0	15.6
Roaring		
Cutthroat	0.6	8.8
Right Fork		
Cutthroat	1.2	12.7
Indian		
Brook	1.0	7.1
Little Green		
Cutthroat	0.0	6.3
Davis		
Brook	0.0	5.5
Brown	0.3	0.4
Total	0.3	5.9
Porcupine[b]		
Brook	0.0	11.7
Cow		
Brook	0.2	8.0
Brown	0.8	2.3
Total	1.0	10.3

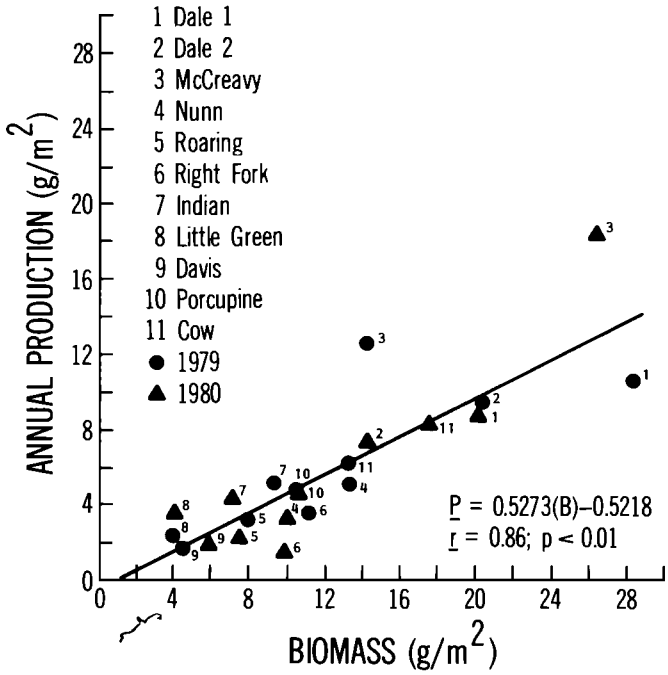
[a] Only the middle three of five population estimates were used.
[b] Only the first four of five population estimates were used.

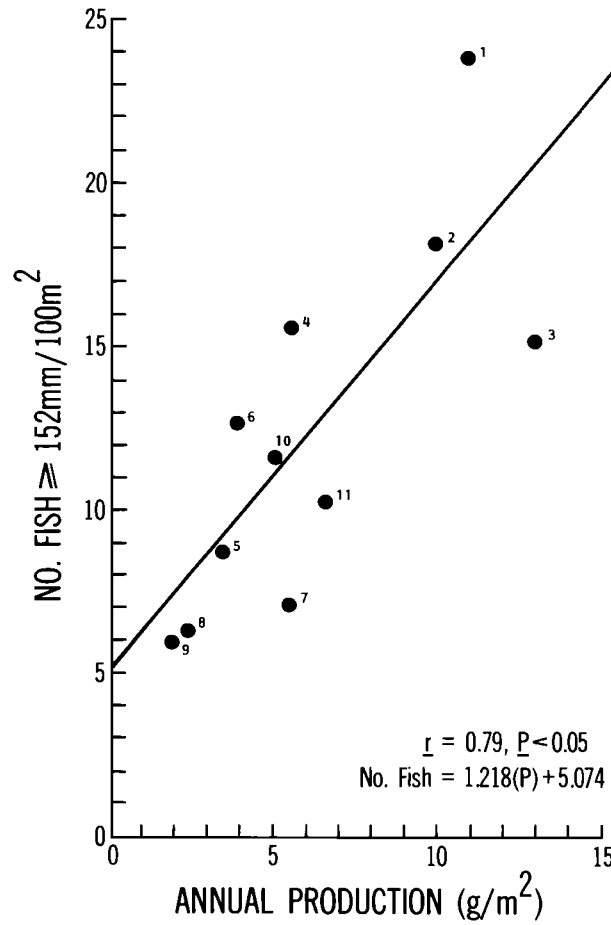
Correlations

There were strong correlations between annual production and midsummer biomass and between production in 1979 and the density of fish at least 152 mm long in 1979 and 1980 (Figure 2). In essence, streams with the high standing crops tended to have the higher production and higher densities of larger fish desired by anglers. Production was inversely related to elevation (Figure 3) and directly related to substrate diversity and conductivity (Figure 4), as well as hardness (r^2 = 0.22;

→

FIGURE 2.—Relationships of midsummer trout biomass (above) and average density of fish at least 152 mm long (below) to trout production for 10 streams in northern Colorado, 1979 and 1980.


1 Dale 1
2 Dale 2
3 McCreavy
4 Nunn
5 Roaring
6 Right Fork
7 Indian
8 Little Green
9 Davis
10 Porcupine
11 Cow
● 1979
▲ 1980
P = 0.5273(B)–0.5218
r = 0.86; p < 0.01
ANNUAL PRODUCTION (g/m2)
BIOMASS (g/m2)
0
4
8
12
16
20
24
28


r = 0.79, P<0.05
No. Fish = 1.218(P)+5.074
NO. FISH ≥ 152mm/100m2
ANNUAL PRODUCTION (g/m2)
0
5
10
15
20
25

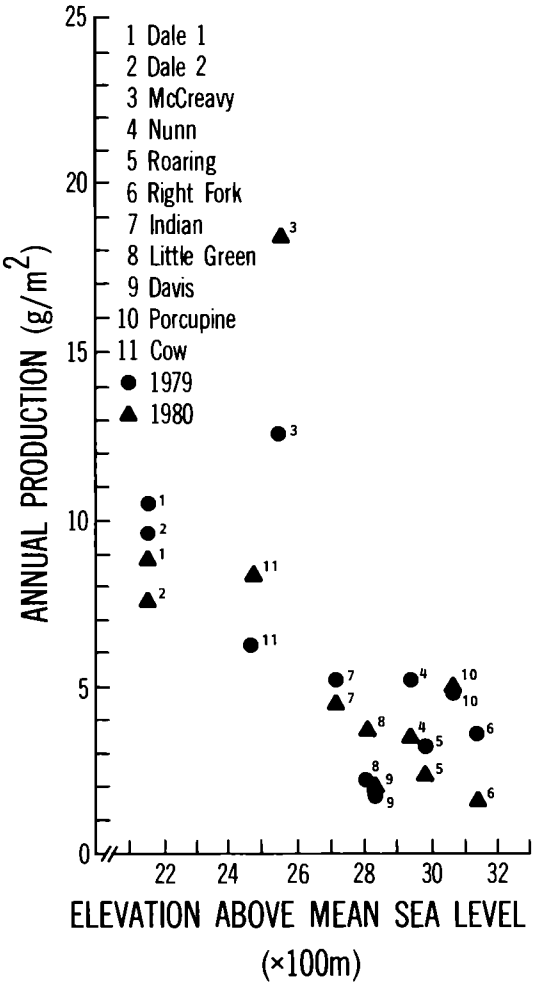


FIGURE 3.—Inverse relationship between elevation above sea level (in hundreds of meters) and trout production for 10 streams in northern Colorado, 1979 and 1980.

$P < 0.05$), and alkalinity ($r^2 = 0.19$; $P < 0.05$; Table 8). No significant correlations were found between production and any of the other physical and chemical factors. Of the five variables significantly related to production, four (elevation, alkalinity, hardness, and conductivity) were closely correlated among themselves; only diversity of substrate was independent of the others.

The stepwise regression analyses, which eliminated closely related variables, produced several different combinations of variables that explained similar percentages of the variations in production and biomass (Table 8). For two-variable combinations, the elevation and width : depth ratio explained 60% of the variation in production; elevation and discharge explained 55% and elevation and substrate diversity 54%. Three-variable permutations of elevation, substrate diversity, mean velocity, width, width : depth ratio, and percentage of zero-velocity stations explained 77–79% of the variation in production. The four-variable combination of alkalinity, elevation, mean width, and width : depth ratio explained 83% of the variation in production, and other four-variable combinations worked nearly as well (Scarnecchia 1983).

Like production, midsummer biomass of fish in the 11 sections (Table 8) was inversely related to elevation ($r^2 = 0.46$; $P < 0.01$) and directly related to substrate diversity ($r^2 = 0.37$; $P < 0.01$), conductivity ($r^2 = 0.30$; $P < 0.01$), hardness ($r^2 = 0.24$; $P < 0.05$), and alkalinity ($r^2 = 0.21$; $P < 0.05$). The two-variable combination of elevation and substrate diversity explained 60% of the variation in biomass; elevation and conductivity explained 56%. The three-variable combinations of elevation, substrate diversity, and either undercut banks or width : depth ratio explained 67% of the variation in biomass. A four-variable model (elevation, width : depth ratio, width, alkalinity) explained 82% of the variation in biomass.

The density of fish at least 202 mm long was related directly to conductivity ($r^2 = 0.67$; $P < 0.01$) but inversely to elevation ($r^2 = 0.52$; $P < 0.05$). Similar, but less close relationships held for fish 152 mm or longer: conductivity, $r^2 = 0.44$ ($P < 0.05$); and elevation, $r^2 = 0.36$ ($P < 0.05$).

HQI and Biomass of Trout

Estimated habitat quality indices for the 11 sections are presented in Table 9; overall, they were significantly related to biomass of trout in 1979 ($r^2 = 0.44$; df = 9; $P < 0.05$) but not in 1980 ($r^2 = 0.16$; $P > 0.05$). For some creeks (Nunn, Little Green), the HQI estimates effectively predicted biomass but for some others they were either far too high (Dale and Davis) or far too low (McCreavy).

Discussion

Factors Related to Production

Elevation, conductivity, alkalinity, hardness, and substrate diversity were significantly related to trout production and biomass in the 11 stream sections studied. Elevation, which explained more of the variation in production and biomass than any other single variable, was especially useful for predicting production and biomass locally because it could be easily estimated from maps. Crisp et al.

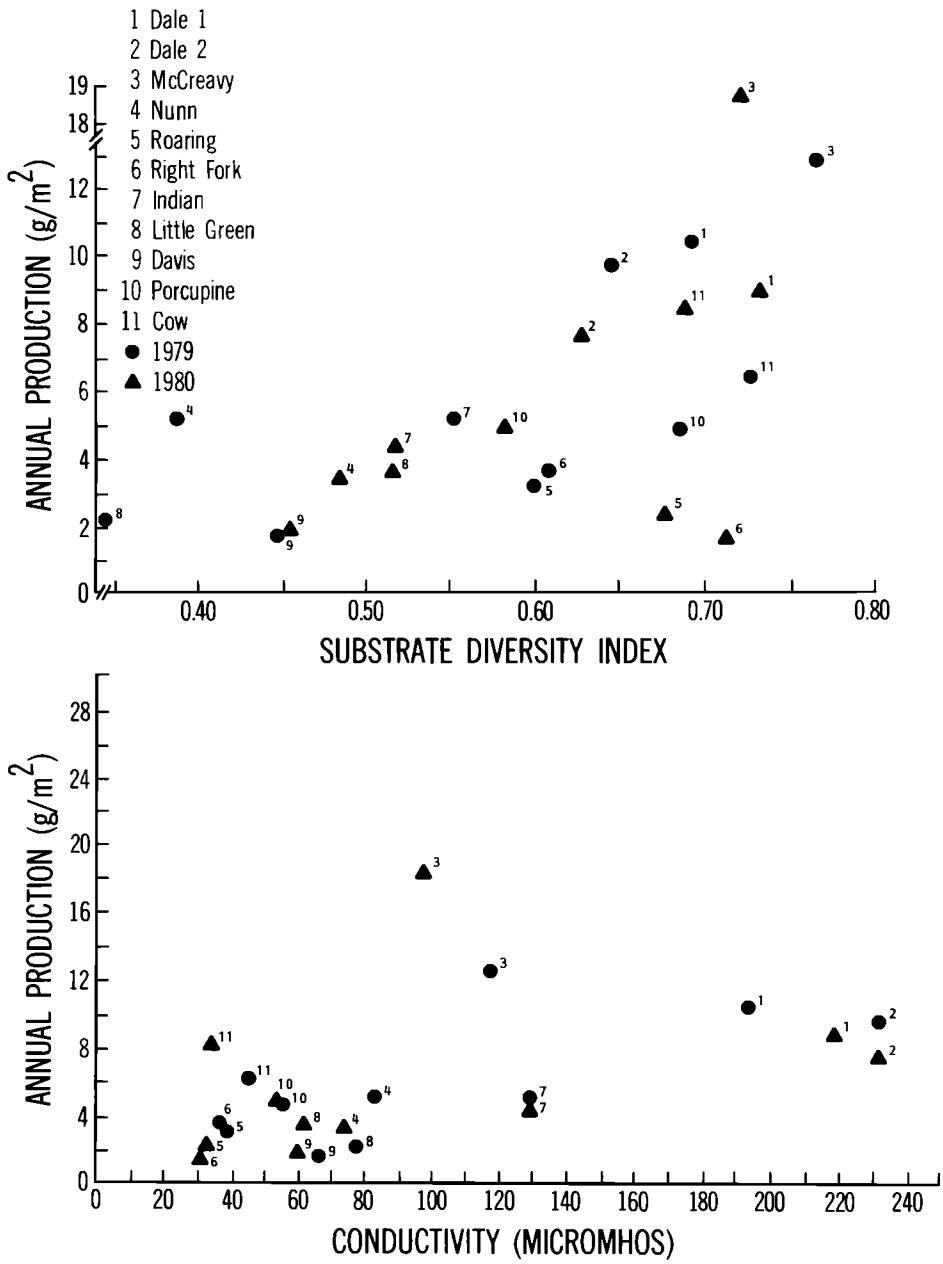


FIGURE 4.—Relationships of substrate diversity (above) and conductivity (below; μmhos = μS) to trout production for 10 streams in northern Colorado, 1979 and 1980.

(1975) found that production of brown trout in tributaries of the River Tees, England, decreased with increasing elevation. For a wider range of elevations at a given latitude, however, a dome-shaped rather than a linear relationship between elevation and production may result. For example, Burton and Wesche (1974) found a direct relationship between biomass per unit area and elevation, the opposite of our findings. Their direct relationship seemingly resulted from their inclusion of several low-elevation streams that have only marginal habitat for trout and contained many warmwater fish. Because trout production may decrease at low elevations (or latitudes) as stream

TABLE 8.—Simple and multiple regression relationships of trout production and biomass to physical and chemical variables in 10 streams in northern Colorado, 1979 and 1980 combined.

Variables	Variation explained (r^2 or R^2)	Equation
	Production (P)	
Elevation (E)	0.42	$P = -0.00795E + 27.4340$
Substrate (S)	0.34	$P = 19.7970S - 5.98343$
Conductivity (C)	0.24	$P = 0.03032C + 3.01391$
Hardness (H)	0.22	$P = 0.05762H + 3.05809$
Alkalinity (A)	0.19	$P = 0.05293A + 3.03973$
Elevation, width : depth ratio (WD)	0.60	$P = -0.0101E - 0.1781WD + 36.8387$
Elevation, percentage of 0-velocity stations (V_0)	0.56	$P = -0.0110E + 0.0978V_0 + 29.8050$
Elevation, discharge (D)	0.55	$P = -0.0118E - 38.3702D + 39.5668$
Elevation, substrate	0.54	$P = -0.0061E + 13.3891S + 14.4318$
Elevation, percentage of 0-velocity stations, substrate	0.79	$P = 0.0096E + 0.1344V_0 + 18.7097S + 12.5224$
Elevation, substrate, mean velocity ($\bar{V}$)	0.77	$P = -0.0086E + 21.4689S - 41.7295\bar{V} + 20.8457$
Elevation, width : depth ratio, mean width ($\bar{W}$)	0.77	$P = -0.0117E - 0.2444WD - 0.5252\bar{W} + 49.4334$
Elevation, width : depth ratio, alkalinity	0.77	$P = -0.0190E - 0.2855WD - 0.0947A + 68.0815$
Elevation, substrate, percentage of 0-velocity stations, undercut banks (U)	0.84	$P = -0.0088E + 20.1802S + 0.1342V_0 - 0.2010U + 11.9412$
	Mean biomass ($\bar{B}$)	
Elevation	0.46	$\bar{B} = -0.01356E + 48.83390$
Substrate	0.37	$\bar{B} = 33.3828S - 7.95697$
Conductivity	0.30	$\bar{B} = 0.05435C + 6.90656$
Hardness	0.24	$\bar{B} = 0.9721H + 7.28789$
Alkalinity	0.21	$\bar{B} = 0.9050A + 7.10545$
Elevation, width : depth ratio, mean width, alkalinity	0.82	$\bar{B} = -0.170E - 0.2934WD - 0.3543\bar{W} - 0.0622A + 65.8648$
Elevation, substrate	0.60	$\bar{B} = -0.0105E + 22.3787S + 27.1019$
Elevation, conductivity	0.56	$\bar{B} = -28.7676E + 0.0446C - 9.4448$
Elevation, hardness	0.55	$\bar{B} = -30.8427E + 0.855H - 10.6648$
Elevation, width : depth ratio	0.54	$\bar{B} = -0.0159E - 0.1898WD + 58.86$
Elevation, substrate, undercut banks	0.67	$\bar{B} = -0.0090E + 25.2285S - 0.3872U + 25.9761$
Elevation, substrate, width : depth ratio	0.67	$\bar{B} = -0.0128E + 20.9473S - 0.1671WD + 37.3129$

temperatures become too high, the investigator should be aware that elevation can confound factors such as latitude and average or maximum summer temperatures.

High alkalinity, hardness, and conductivity resulted in increased production of salmonids in our streams, as in other streams worldwide. Mortensen (1977) reported that production of brown trout and nonsalmonid fishes in seven Danish streams was higher in streams with relatively high conductivities. English chalk streams, high in calcium, had three to nine times greater fish production than streams low in calcium, even though most of that production was contributed by nonsalmonids (Le Cren 1969). O'Connor and Power (1976) concluded that brook trout production in eight eastern North American streams increased with increasing conductivity. Both instantaneous growth rates of brown trout and biomass of all fish species inhabiting six Pennsylvania streams were positively correlated with stream conductivities (McFadden and Cooper 1962). The high biomass and production of salmonids at high conductivities results, in part, because of more food organisms. Egglishaw (1968) reported that biomass of benthic organisms per gram of plant detritus in eight Scottish streams was positively correlated with conductivity.

Alkalinity, hardness, and conductivity—like elevation—are easily measured. However, in many salmonid streams, chemical influences on production over narrow ranges of variation may be dominated or obscured by physical habitat influences such as cover, except when one compares a relatively sterile stream such as Right Fork with chemically richer streams such as Dale Creek. Also, because these three chemical factors are correlated among themselves and with elevation, the measurement of one of the three may usually be ad-

TABLE 9.—Habitat quality index (HQI) estimates of trout biomass (g/m^2), observed midsummer biomasses, and their differences for 10 northern Colorado streams, 1979 and 1980.

Stream	1979[a]			1980[b]		
	HQI	Observed	Difference	HQI	Observed	Difference
Dale 1	33.8	28.2	5.6	43.5	20.1	23.4
Dale 2	36.3	20.3	16.0	43.5	14.3	29.2
McCreavy	9.8	13.3	−3.5	1.2	22.7	−21.5
Nunn	2.8	5.2	−2.4	1.0	3.4	−2.4
Roaring	16.3	7.9	8.4	16.3	7.5	8.8
Right Fork	31.5	11.1	20.4	31.5	8.9	22.6
Indian	2.1	8.0	−5.9	1.3	7.1	−5.8
Little Green	5.5	3.9	1.6	2.4	4.0	−1.6
Davis	24.2	4.0	20.2	19.4	5.6	13.8
Porcupine	24.5	10.4	14.1	19.1	10.6	8.5
Cow	23.1	13.2	9.9	23.1	17.6	5.5

[a] Observed biomass = 0.390(HQI) + 3.958; $r^2 = 0.44$; $P < 0.05$.
[b] Observed biomass = 0.164(HQI) + 8.066; $r^2 = 0.16$; $P > 0.05$.

equate. Once elevation is known, less information may result from measuring the others than if each was measured alone.

The overall weakness (despite statistical significance) of the correlations of chemical factors with production suggested to us that physical factors strongly influence production in these streams. Many of these physical factors are related to cover, such as boulders, debris, logs, deep water, and turbulence that require detailed and subjective appraisal by experienced personnel. For example, Dale Creek had few undercut banks but had many other types of cover such as rocks, deep water, and brush. Although detailed evaluations of cover may not be practical in most small streams, an overall percent cover rating such as that used by Binns and Eiserman's (1979) model II may enable cover to be estimated within a reasonable period of time.

Some physical factors measured in this study were related to production. For example, production increased with increasing diversity of substrates (Figure 4). Small fish distribute themselves differently from large fish according to velocities and the resulting substrates. Griffith (1972) reported that young brook trout and cutthroat trout in Idaho streams occupied shallower water than older fish. Such partitioning of habitat lessens the competition between age-groups and leads to higher production. Mortensen (1977) found that production of brown trout was highest in streams in which both young of the year and yearlings accounted for substantial production.

Different variables often limit production in different streams. Limiting factors also may change yearly in a given stream, according to the environment as well as to the age structure of the population. In our analysis, the variables not correlated with previously entered variables such as elevation, but which explained remaining variation in production, were most likely to enter the stepwise regression models. For example, the width : depth ratio, which by itself was not significantly related to production ($r^2 = 0.02$; $P > 0.05$), was the most important variable explaining variation in production, after elevation was included in the stepwise model. This result is consistent with Mortensen's (1977) finding that lower width : depth ratios in Brandstrup Beck and Mausing Mollebeck, Denmark, were associated with higher production of salmonids. Production of brown trout in Bere Stream, England, also increased as the width : depth ratio decreased (Le Cren 1969). A lower ratio results in more production per unit of surface area partly because fish production involves growth and survival in three dimensions, whereas production is usually expressed in two dimensions. Deep small streams thus are often more productive per unit of area than are shallower small streams of equal area.

Elevation, percentage of zero-velocity stations, and substrate diversity were the three most effective combinations of variables for explaining variation in production. Elevation, substrate diversity, and mean velocity followed closely. The high percentage of zero-velocity stations in our streams provided more habitat for young trout, which have high ratios of production to biomass. We observed that young fish tended to remain near the edges of streams; Latta (1969) observed similar behavior by young brook trout in the Pigeon River, Michigan.

Preferably, factors that cause the variation in

TABLE 10.—Effective combinations of variables for predicting trout production in Colorado's small streams. A maximum summer temperature of less than 23°C is assumed.

Number of variables	Suitable combinations	Range of applicability for added variable
1	Elevation	2,000–3,000 m
2	Elevation and width : depth ratio	5–50
3	Elevation, width : depth ratio, and alkalinity	0–120 mg/L
4	Elevation, width : depth ratio, alkalinity, and mean width	<6 m

production and biomass should be used in prediction equations. Because correlation analysis does not indicate which factors cause a response, it is not possible to unequivocally determine which physical or chemical factors cause the variations in production or biomass and which factors merely accompany these changes. Nevertheless, our results indicate that production and biomass in these small Colorado streams were related to some easily measured physical and chemical factors. We list some of the combinations of variables in Table 10 that, in our judgment, can be used to effectively estimate the general level of production that can be expected, as judged by their probable causal connection to production and the ease and inexpensiveness of their measurement. The regressions should be applied only to streams with variables in or near the ranges of those in our streams. Even without extrapolating beyond conditions on which the equations are based, however, our relationships can be used to estimate production and standing crop in many of Colorado's small streams (orders 1–3) that are apt to be fished.

HQI Evaluation

We believe that the limited success in applying HQI model II to our biomass estimates resulted from three causes which we briefly discuss here: (1) lack of exact measurements of some habitat variables according to the methods of Binns (1982) and Binns and Eiserman (1979); (2) the inability of model II, a less demanding model than others in terms of data required, to account for subtleties in habitat and differences between geographical areas that sometimes greatly influence biomass and production; and (3) the smallness of our streams relative to those from which the HQI model was developed.

First, our estimates of several variables required by the HQI model were based on our own habitat measurements and not done as outlined by Binns (1982). Despite our best attempts to classify habitats according to his methods, unintended differences in measurement and interpretation may have occurred. The overestimates of biomass in Dale 1 and Dale 2 with the HQI were especially obvious. Most of our HQI estimates were too high, which indicated that our ratings were probably too liberal. Carefully documented manuals (Binns 1982) are helpful, but interjurisdictional communication and workshops are needed to produce standardized procedures.

Secondly, several other HQI estimates for our streams missed the observed standing crop estimates by wide margins. In Davis Creek, for example, the predicted biomass was over six times the observed biomass in 1979 and almost four times the observed value in 1980. From initial and subsequent observations, we would have supposed Davis Creek to be excellent brook trout habitat because the banks were stable and instream cover (logs, rocks, deep water) appeared to be abundant (Scarnecchia 1983). However, the maximum summer temperature was only 10.5°C in 1979 and 13.0°C in 1980. We are not certain how long these maximum temperatures persisted in Davis Creek, but the poor condition of the fish compared to that of all other brook trout stocks that we investigated indicated that the temperatures in Davis Creek were several degrees below those that promote optimal growth and production. The HQI model II, however, characterized the "best" class of temperatures as 12.6 to 18.6°C; the 10.5° and 13.0°C in Davis Creek were thus classified as 3 (good) or 4 (best).

Porcupine Creek was also rated by its HQI at twice the biomass that we observed. Its maximum temperatures (14.5° and 17.0°C) in 1979 and 1980 were rated as 4 (best). Yet growth and the size of the young brook trout were much lower in this creek than in several others. The average weight of yearling fish was only 3.1 g after two full growing seasons. In contrast, yearling brook trout of the same age in Dale and Indian creeks averaged 30.7 and 15.8 g, respectively. Maximum temperature data only grossly estimate thermal conditions in the streams. In our view, the duration of an optimal range of temperatures and the size of the fish before they enter their first winter would better indicate potential for growth, and hence biomass and production. Davis and Porcupine creeks are high-elevation streams (2,835 and 3,066 m, re-

spectively) in large mountain ranges and have heavily forested watersheds, whereas Dale and Indian creeks are lower and have longer periods of optimal instream temperatures. Optimal summer temperatures probably occur only briefly in Davis and Porcupine creeks during the short growing seasons; thus, the benefits to production are badly overrated by the HQI model. Binns (1982) also recognized that HQI indices were highly sensitive to different ratings for maximum temperature.

Finally, five of our streams were smaller than any of the 44 streams used by Binns and Eiserman (1979) for developing the HQI and the rest of our streams were near the low end of the size range. McCreavy Creek posed a unique problem among all of the streams: in 1980, the HQI estimate was only 5% of the observed biomass. Although this creek is only 0.6 m wide and its velocities are among the lowest measured in our streams, it is the deepest for its width of any of our streams. Partly because of this greater depth, McCreavy Creek supported a substantial biomass of brook trout and even some large brown trout (Table 7). Reproduction also was substantial in McCreavy Creek and growth of young-of-the-year brook trout was good. Many age-classes were represented (Scarnecchia 1983). Most streams of McCreavy Creek's width in northern Colorado hold few or no fish, and certainly no harvestable ones. Such distinctiveness points out the difficulty of effectively estimating habitat quality and standing crop in certain small streams without extensive physical, chemical, and biological sampling.

Evaluating Small Stream Habitats and Populations

Our results showed that our more productive study streams were characterized by high midsummer trout biomass (Figure 2); therefore, biomass served adequately as an effective estimate of production. Anglers also could expect to find a higher density of fish of a desirable size in streams with higher production. Elevation and conductivity data effectively predicted the biomass of desirable fish. Total production and biomass, as well as the density of fish of desirable size, would change under more intensive harvest. In practice, it may be necessary to assume, for more heavily fished streams, that sustainable yield is a percentage of the average annual production, or apply a yield model such as Ricker's (1975) method for equilibrium yield.

Detailed habitat evaluations in small streams are time consuming and expensive. The large number of streams to be evaluated makes it infeasible to evaluate all of them unless a simplified method is developed. Our approach, as well as those of Binns and Eiserman (1979) and Burton and Wesche (1974), are attempts to develop simple methods of assessment. No matter which assessment method is used, some streams will not fit the simple relationships. For the present, and for many small streams, obtaining a philosophical commitment from landowners and the public to perpetuate the natural character of small streams may be more relevant than detailed analyses of each stream's characteristics for the management of a fishery. The option of more detailed studies, if needed, will then be preserved.

Acknowledgments

This project was jointly supported by the Colorado Division of Wildlife, the U.S. Fish and Wildlife Service, and Colorado State University. We thank the Sport Fishing Institute and the National Wildlife Federation for providing additional financial support. S. Horak and M. Giossi assisted with the fieldwork, and P. Campana assisted with the laboratory work. We also thank R. Behnke, N. A. Binns, and R. Carline for their constructive comments.

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ERRATA -- Scarnecchia, D. L., and E. P. Bergersen. 1987. Trout production and standing crop in Colorado's small streams, as related to environmental features. North American Journal of Fisheries Management 7: 315-330.

Page 318 -- Table 1. McCreavy Creek sampling date. For "July 14", read "July 17".

Page 319 -- Table 2. Under "Range" for Cow Creek. For "97-100", read "79-100".

Page 324 -- Paragraph 1 For "nearly as well" read "about as well".

Page 324 -- Paragraph 2 Under "elevation and conductivity explained 56%" read "substrate and conductivity explained 56%". Delete sentence "A four variable model (elevation, width:depth ratio, width, alkalinity) explained 82% of the variation in biomass".

Page 326 -- Table 8. Substitute Table 8 below for original Table 8.

In addition, two of our production equations in Table 8 have the variable alkalinity entering stepwise models with a sign (-) opposite to that expected from our discussion. Care should be taken in applying these equations to other situations.

The authors regret any confusion these errors may have caused.

Table 8. Simple and multiple regression relationships between trout production and biomass, physical and chemical variables, in 10 streams in northern Colorado, 1979 and 1980 combined.

Variables	Variation explained (r^2 or R)	Equation
	Production (P)	
Elevation (E)	0.42	$P = -0.00795\ (E) + 27.4340$
Substrate (S)	0.34	$P = 19.7970\ (S) - 5.98343$
Conductivity (C)	0.24	$P = 0.03032\ (C) + 3.01391$
Hardness (H)	0.22	$P = 0.05762\ (H) + 3.05809$
Alkalinity (A)	0.19	$P = 0.05293\ (A) + 3.03973$
Elevation, width:depth ratio (WD)	0.60	$P = -0.0101\ (E) - 0.1781\ (WD) + 36.8387$
Elevation, percent of 0-velocity stations (V_o)	0.56	$P = -0.0110\ (E) + 0.0978\ (V_o) + 29.8050$
Elevation, discharge (D)	0.55	$P = -0.0118\ (E) - 38.3702\ (D) + 39.5668$
Elevation, substrate	0.54	$P = -0.0061\ (E) + 13.3891\ (S) + 14.4318$
Elevation, percent of 0-velocity stations, substrate	0.79	$P = -0.0096\ (E) + 0.1344\ (V_o) + 18.7097\ (S) + 12.5224$
Elevation, substrate, mean velocity ($\bar{V}$)	0.77	$P = -0.0086\ (E) + 21.4689\ (S) - 41.7295\ (\bar{V}) + 20.8457$
Elevation, width:depth ratio, mean width ($\bar{W}$)	0.77	$P = -0.0117\ (E) - 0.2444\ (WD) - 0.5252\ (\bar{W}) + 49.4334$
Elevation, width:depth ratio, alkalinity	0.77	$P = -0.0190\ (E) - 0.2855\ (WD) - 0.0947\ (A) + 68.0815$
Elevation, width:depth ratio, mean width, alkalinity	0.83	$P = -0.0170\ (E) - 0.2934\ (WD) - 0.3543\ (\bar{W}) - 0.0622\ (A) + 65.8648$
Elevation, substrate, percent of 0 velocity stations, undercut banks (U)	0.84	$P = -0.0088\ (E) + 20.1802\ (S) + 0.1342\ (V_o) - 0.2010\ (U) + 11.9412$

Table 8. Continued

Variables	Variation explained (r^2 or R)	Equation
	Biomass (B)	
Elevation	0.46	B = - 0.01356 (E) + 48.83390
Substrate	0.37	B = 33.3828 (S) - 7.95697
Conductivity	0.30	B = 0.05435 (C) + 6.90656
Hardness	0.24	B = 0.09721 (H) + 7.28789
Alkalinity	0.21	B = 0.09050 (A) + 7.10545
Elevation, substrate	0.60	B = - 0.0105 (E) + 22.3787 (S) + 27.1019
Substrate, conductivity	0.56	B = + 28.7676 (S) + 0.0446 (C) - 9.4448
Substrate, hardness	0.55	B = + 30.8427 (S) + 0.0855 (H) - 10.6648
Elevation, width:depth ratio	0.54	B = - 0.0159 (E) - 0.1898 (WD) + 58.86
Elevation, substrate, undercut banks	0.67	B = - 0.0090 (E) + 25.2285 (S) - 0.3872 (U) + 25.9761
Elevation, substrate, width:depth ratio	0.67	B = - 0.0128 (E) + 20.9473 (S) - 0.1671 (WD) + 37.3129