

## Variation in Condition of Rainbow Trout in Relation to Food, Temperature, and Individual Length in the Green River, Utah

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**Abstract.**—We examined how condition (weight at length) of rainbow trout *Oncorhynchus mykiss* varied in relation to availability of drifting invertebrates and temperature at two locations over four seasons in the Green River, Utah. Food availability (daytime drift density) varied more than 17-fold across sites and seasons, and rainbow trout experienced an 11°C range in mean monthly temperature. Both rainbow trout gut fullness and condition increased as joint, nonlinear functions of increasing food availability and increasing temperature. Variation in condition decreased with fish size, although condition of intermediate sized fish was most strongly related to variation in food and temperature. Observed relationships between rainbow trout condition, drift abundance, and temperature were qualitatively consistent with bioenergetic models that predict fish growth should vary as a joint function of food and temperature. However, the inferred temperature optima for rainbow trout seemed to be significantly higher than predicted. Our results support a growing body of evidence that stream trout may be frequently food-limited in nature.

Bioenergetic models predict that fish growth should vary as a joint function of ration and temperature (e.g., Hewett and Johnson 1992). In general, the effect of varying food quantity on growth should be greatest at optimum temperatures, and the effect of varying temperature should be small under conditions of low food supply and increase as amount of food available to individual fish increases. Although most species of stream trout feed primarily on invertebrate drift (Jenkins et al. 1970; Elliott 1970, 1973; Metz 1974; Allan 1981; McNicol et al. 1985), composition and quantity of trout diets can vary markedly among wild populations of trout (e.g., Bisson 1978; Allan 1981). Furthermore, some studies have shown trout growth, abundance, or production to be correlated with food availability (e.g., Slaney and Northcote 1974; Murphy et al. 1981; Hawkins et al. 1983; Fausch 1984; Wilzbach 1985; Cada et al. 1987; Ensign et al. 1990; Hughes and Dill 1990). Although trout growth is jointly controlled by food and temperature in the laboratory (Brett et al. 1969; Elliott 1975a, 1975b, 1979), few data exist demonstrating such relationships under field conditions.

Streams with strong spatial and temporal gradients in drift availability and temperature provide a means of testing if trout growth is limited by both food and temperature and how well current

bioenergetic models describe trout growth under field conditions. Impounded rivers exhibit especially strong gradients of this type (Pearson 1967; Ward 1974; Armitage 1978; White and Wade 1980). In this study, we sought to determine if condition (weight at length) of rainbow trout *Oncorhynchus mykiss* in the Green River below Flaming Gorge Dam, Utah, was related to spatial and seasonal differences in food availability and temperature.

### Study Area

This study was conducted in the first 12.5 km of the Green River below Flaming Gorge Dam in northeastern Utah. The tailwater has a mean elevation of 1,672 m and an average channel slope of 1.6 m/km. Channel widths in this section vary between 40 and 50 m. Habitat consists primarily of long runs and short riffles interspersed with eddies and a few deep pools. Discharge during the study ranged from 22.7 to 119.2 m<sup>3</sup>/s, and flows were highest in winter.

Temperature in the tailwater is regulated to enhance trout growth. Multilevel intake structures in the reservoir allow water to be withdrawn from different depths, resulting in summer temperatures that are close to optimal (12–14°C) for trout growth (Johnson et al. 1987). During winter, the warmest water available in the reservoir (4°C) is released into the tailwater to minimize thermal stress on trout.

Food sources in the tailwater are abundant. Benthic invertebrate biomass ranged from about 4 to 7.5 g dry matter/m<sup>2</sup> during the 1981 water-year

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(Johnson et al. 1987). However, invertebrate diversity is low, and seven taxa account for about 90% of total numbers. Dominant taxa throughout the study area included *Baetis* spp. and *Ephemerella* spp. (Ephemeroptera), *Hydroptila* spp. (Trichoptera), *Simulium* spp. (Diptera), Chironomidae, *Hyalella* spp., and Oligochaeta.

The tailwater fishery is dominated by rainbow trout, but cutthroat trout *Oncorhynchus clarki*, brook trout *Salvelinus fontinalis*, and brown trout *Salmo trutta* are also present (Modde et al. 1991). During the study period, mean biomass densities of rainbow trout, brook trout, cutthroat trout, and brown trout near the tailrace (site 1) were 695, 84, 58, and 0 kg/ha. At Little Hole (site 2), located approximately 11.5 km below the dam (kmbd), corresponding mean densities were 419, 0, 80, and 0.5 kg/ha. Up to the time of this study, recruitment of all species except brown trout was largely supported by stocking. Large fingerlings (average length, 150 mm) are stocked annually in May and reach 300 mm by November of the same year. Around the time of this study (1985–1988), between 100,000 and 120,000 fingerlings were stocked each year. The river is managed as a trophy fishery with a possession limit that favors removal of small trout. The daily limit is two trout shorter than 330 mm and one trout longer than 508 mm.

### Methods

**General sampling design.**—We used a comparative approach to derive empirical relationships between drift, temperature, and rainbow trout weight. We collected data each season (late October 1987, early February 1988, mid-May 1988, and mid-July 1988) from two sites. Although data were collected from two to four pool–riffle pairs for each site–season combination, data were statistically pooled before analysis to give eight sets of observations. We pooled data in this manner because we were interested in differences among sites and seasons, not within sites.

**Sampling locations and times.**—Two reaches (sites) were sampled. Site 1 included the first 2.2 km of river below the dam (bd), and site 2 extended from 10.5 to 12.1 kmbd.

To minimize confounding effects of daily variation in discharge on relationships between drift and rainbow trout feeding, we sampled each site during a 48-h period of stable flow. Discharge from the dam was held nearly constant by the U.S. Bureau of Reclamation (USBOR) 24 h before and throughout each sampling period. Stable discharges equaled the weighted mean of the average daily

TABLE 1.—Locations and times of data collection in this study. At each site and time, three invertebrate drift samples were collected from a riffle, and between 45 and 73 rainbow trout were collected from the pool immediately downstream. Sites were in the Green River below Flaming Gorge Dam (kmbd = kilometers below dam).

Site and location (kmbd)	Collection time	
	Fall 1987	Winter, spring, summer 1988
Site 1		
0.3	1 h before sunrise	45 min after dawn
2.0	1100 hours	1330 hours
0.3	1700 hours	30 min after complete darkness
2.0	2230 hours	0130 hours
Site 2		
10.5	2230 hours	45 min after dawn
11.2	1 h before sunrise	1330 hours
11.8	1100 hours	30 min after complete darkness
12.0	1700 hours	0130 hours

and nightly flows predicted from the historical, postdam record for that time of year.

During each season, we sampled pools for rainbow trout and sampled riffles above each pool for drifting invertebrates. We collected data early in the morning, around midday, at dusk, and late at night (Table 1). Discrepancies in sampling times between fall and the other seasons occurred because the USBOR was unable to schedule stable discharges at precisely the requested time during fall 1987. Because only two pools (0.3 and 2.0 kmbd) were accessible at site 1, we sampled each habitat pair twice during each season but alternated sampling of these locations within the 24-h period. At site 2 we sampled four separate pool–riffle pairs.

**Drifting invertebrates.**—Each drift collection consisted of three 10-min samples taken consecutively along a partial transect of the river at depths of 1.0, 0.75, and 0.5 m. Drifting invertebrates were collected with cone-shaped nets that were secured to steel rods driven into the substrate. The nets were 0.9 m long with an aperture area of 0.09 m<sup>2</sup> and a mesh size of 450  $\mu$ m. The center of each net was set at 60% of the depth of the water column, the approximate location of average current velocity (Platts et al. 1983). Water velocity was monitored with a mechanical flowmeter (General Oceanics model 20307) mounted in the center of the net aperture by cords attached to the net frame. All samples were preserved in 70% ethanol for later analysis.

In the laboratory, all invertebrates longer than 1 mm were identified and counted. Total volumes

were measured by displacement in a graduated cylinder for each combination of site, season, and time period. We calculated drift density (DD) as numbers/100 m<sup>3</sup> of water after Allan and Russek (1985):

$$DD = \frac{\text{numbers/net-hour}}{\text{m}^3 \text{ filtered/net-hour}} \times 100. \quad (1)$$

Drift volume was calculated in a similar manner as milliliters of invertebrates/100 m<sup>3</sup> of water filtered.

**Rainbow trout diets.**—About 5 min after sampling the drift from a riffle, we captured rainbow trout in the downstream pool by electrofishing from a jet boat. Immediately after capture, rainbow trout were killed with tricaine methanesulfonate. The location, date, approximate time of capture, total length (TL, nearest millimeter) and weight (nearest gram) were recorded for each fish before the gut was removed and stored in 70% ethanol. For each combination of site and season, we captured 45–73 rainbow trout 200–500 mm long.

In the laboratory, invertebrates were removed from the portion of the gut between the anterior of the esophagus and the pyloric sphincter (Kimball and Helm 1971). Invertebrates from each stomach were identified in the same manner as those from drift samples. The volume (mL) of invertebrates in each stomach was measured with a graduated cylinder, and relative gut volume (RGV) was calculated as

$$RGV = \frac{\text{invertebrate volume (mL)}}{\text{fish TL (m)}}. \quad (2)$$

**Water temperature.**—Continuous temperature data were available only for site 1 during this study. However, Johnson et al. (1987) used thermographs to record daily maximum and minimum water temperatures at each study site during 1980. Mean daily temperatures at site 1 for the 1988 water-year were highly correlated with those at site 1 during the 1980 water-year. We assumed that differences in temperature between the two sites would be similar for the two water-years, and we used a regression equation relating temperature at site 2 ( $T_2$ ) to temperature at site 1 ( $T_1$ ) from the 1980 data ( $T_2 = -0.917 + 1.182 T_1$ ;  $r^2 = 0.94$ ,  $N = 366$ ) to estimate mean daily temperatures at site 2 during the 1988 water-year.

We then summarized temperature data in two ways. First, mean daily temperatures were used to calculate mean annual temperature and total accumulated degree-days for each site. We also calculated the mean temperature at each site during

the 30 d before each sampling date, hereafter referred to as T30. A 30-d period was used because it is long enough for measurable rainbow trout growth to occur and short enough to reflect seasonal differences in thermal conditions.

**Rainbow trout weight.**—Linear regression was used to estimate parameters for the logarithmic form of the length–weight relationship for each group of rainbow trout collected at a site and season where

$$\log_{10}(W) = \log_{10}(a) + b \cdot \log_{10}(L); \quad (3)$$

$W$  is fish weight (g),  $L$  is fish TL (mm),  $\log_{10} a$  is the y-intercept, and  $b$  is the slope. Before analysis, we subtracted the estimated weight of the stomach contents of each fish. We estimated the wet weight of stomach contents by multiplying the specific gravity of invertebrate prey (1.05; see Wetzel and Likens 1990) by the volume (mL) of prey in the stomach. When we plotted the log of fish weights against log of length, we noticed that some individual fish appeared to be statistical outliers. We excluded from the regressions any observations that Cook's  $D$  statistic identified as outliers (Wilkinson 1992). The numbers of fish excluded from regressions by this procedure ranged from zero to five and in only one case (8%) exceeded 5% of the sample numbers. Analysis of covariance was then used to test if the slopes of the eight separate length–weight relations differed.

We used the eight sample-specific regression models to calculate length-specific rainbow trout weights for each combination of site and season. Values were calculated for lengths between 200 and 500 mm at 25-mm intervals. For most analyses, however, we only present data for 200, 300, 350, 400, and 500-mm fish. These length-specific weight estimates are hereafter referred to as W200, W300, etc. We chose this method of quantifying condition because it avoided the methodological flaws associated with condition factors. Unless slopes of length–weight relationships are equal for each population of interest, condition factors (e.g.,  $K_n$  and Fulton's  $K$ ) provide ambiguous information regarding differences in fish weight at length (e.g., Le Cren 1951; Cone 1989, 1990).

**Statistical summaries.**—Because we were interested in comparisons among sites and seasons, we generated mean values of gut fullness and drift for each site–season combination ( $N = 8$ ). We first calculated within-riffle or within-pool means based on the three drift samples or the total number of rainbow trout captured at a particular combination of season, site, and time of day (Table 2).

This procedure provided two daytime observations and two nighttime observations for both drift and gut fullness for each site and season (Table 2).

We then calculated overall site-by-season means in two ways. First, we calculated mean values of drift and gut fullness based on all four sampling periods ( $N = 4$ ). We then calculated means based on only the two daytime values. We analyzed the latter because rainbow trout are sight feeders, and relationships between trout condition, feeding, and drift availability could have been confounded by diel variation in drift. We were especially concerned that nighttime drift data might obscure real patterns because drift rates are often much higher at night than during the day (see Allan and Russek 1985).

**Hypothesis tests and model building.**—After data aggregation, we used linear regression to determine if differences among sites and seasons in the slopes and intercepts of the length–weight relationships were related to variation in drift density and temperature. For our main analyses, we used drift density rather than drift volume because some volumetric estimates were strongly influenced by the presence of large, rare taxa. We also used daytime drift density rather than overall drift density because of the known diel feeding behavior of rainbow trout.

To test if rainbow trout condition changed as a joint function of drift availability and temperature, we used the product of daytime drift density and T30 (hereafter abbreviated as  $D \times T$ ) as the independent variable in these analyses. To determine if other models provided better predictions of rainbow trout condition, we also conducted a series of regressions that included all seven possible combinations of drift density, T30, and  $D \times T$  as independent variables.

We also regressed each set of estimated weights at length against  $D \times T$  to determine if variation in rainbow trout condition depended on individual size. For these analyses, we followed exactly the same procedure as described earlier.

Research conducted simultaneously with this study (Modde et al. 1991) indicated that rainbow trout, cutthroat trout, brook trout, and total trout densities were higher at site 1 than site 2. In contrast, brown trout were more abundant at site 2. Because trout abundance might have directly influenced individual weight, we used analysis of covariance (ANCOVA) to determine if rainbow trout weight at length was related to unmeasured site-specific factors (e.g., trout density). In this

analysis,  $D \times T$  was the covariate and sites were considered the main treatments.

**Comparison of regression and bioenergetic models.**—We used the equations from the weight at length versus  $D \times T$  regression analyses to construct contour graphs that illustrated how rainbow trout weight at length varied with simultaneous changes in drift density and temperature. These graphs were compared to graphical representations of predictions generated by the general fish bioenergetics model of Hewett and Johnson (1992). This model was parameterized for rainbow trout based on data in From and Rasmussen (1984). We also parameterized the model to calculate weights based on the temperature range occurring in the Green River over a full range of rations.

## Results

### *Variation in Temperature*

During the 1988 water-year, measured water temperatures at site 1 were slightly (7%) cooler than estimated temperatures at site 2 (means = 8.4° and 9.0°C, degree-days = 3,080 and 3,305, respectively). Site 1 showed a 12.8°C and site 2 a 15.1°C annual range in mean daily temperature (Figure 1). Site 1 was slightly warmer during the winter and slightly cooler during the summer than site 2. However, T30 differed nearly sixfold among sites and seasons (Table 2).

### *Variation in Drift*

The mean daytime density of drifting macroinvertebrates (>1 mm long) varied about 18-fold among sites and seasons (Table 2). Other drift variables showed similar trends. Invertebrate drift was nearly always higher at site 2 than at site 1, with the greatest between-site differences occurring during spring and summer. The four drift variables were not always strongly correlated with one another (Table 3). Daytime drift volume was not significantly correlated with any of the other three drift variables. Daytime drift density was associated with seasonal and site-specific differences in T30 ( $r^2 = 0.58$ ,  $P < 0.03$ ).

### *Size Distribution of Rainbow Trout*

Rainbow trout collected during the study ranged from 180 to 540 mm long (Figure 2). Lengths were bimodally distributed with peaks at about 300 and 400 mm.

### *Composition of Diets and Variation in Rainbow Trout Gut Volumes*

Invertebrates constituted essentially the entire diet of the rainbow trout collected during this

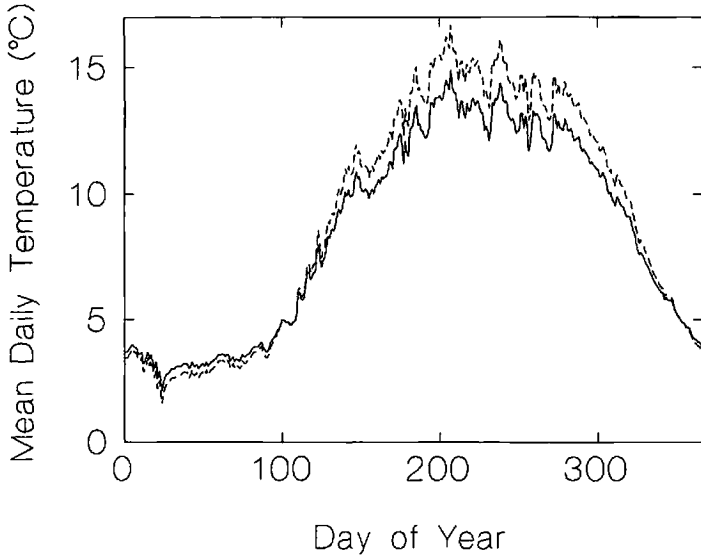


FIGURE 1.—Mean daily temperature at site 1 (solid line) and site 2 (dashed line) between January 1 (day 1) and December 31, 1988. Temperatures for site 2 were estimated from the relationship of temperature at site 2 to temperature at site 1 derived from 1980 measurements.

study. Of the 478 fish collected, only 2 contained fish in their guts.

The relative gut volumes of rainbow trout differed markedly between sites and seasons (13- and 8-fold differences for daytime and overall volumes, respectively; Table 2). Daytime and overall gut volumes were highly correlated with one another ( $r = 0.99$ ), and both measures were correlated with all drift variables ( $r = 0.732$  to  $0.808$ ) except overall drift volume.

*Variation in Rainbow Trout Length-Weight Coefficients and Weight at Length*

The slopes of the length-weight relationships differed among sites and seasons (Table 4; AN-

COVA:  $F = 7.689$ ;  $df = 7, 444$ ;  $P < 0.001$ ). Differences in the value of length-weight coefficients were manifested as differences among sites and seasons in weight at length. In general, condition of rainbow trout appeared to decline during winter and increase from spring to summer (Figure 3). However, the magnitude of change in condition varied with site. The decrease in condition during winter was greatest at site 1, and the increases in spring and summer were greatest at site 2.

The intercept ( $\log_{10} a$ ) of the length-weight relationship increased with increasing values of  $D \times T$ , whereas values of the slope ( $b$ ) exhibited a corresponding decrease (Table 5). In both cases,

TABLE 2.—Mean values and standard errors (in parentheses) for macroinvertebrate drift density and volume and rainbow trout gut fullness at each Green River site and for each season. Mean temperatures during the 30 d before sampling (T30) were measured at site 1; those at site two were estimated. For day variables,  $N = 2$ ; and for overall variables,  $N = 4$ .

Site and season	T30 (°C)	Drift density (number, 100 m <sup>3</sup> )		Drift volume (mL/100 m <sup>3</sup> )		Gut volume (mL/m fish total length)	
		Day	Overall	Day	Overall	Day	Overall
Site 1							
Fall	12.2	529 (234)	398 (75)	2.9 (0.72)	6.2 (1.95)	2.9 (1.34)	2.7 (0.58)
Winter	3.3	43 (6)	48 (7)	4.5 (1.45)	0.4 (0.04)	5.4 (2.68)	4.0 (1.45)
Spring	6.7	112 (11)	91 (13)	0.5 (0.02)	1.7 (0.18)	8.5 (3.76)	5.9 (2.15)
Summer	12.5	758 (132)	970 (131)	1.8 (0.33)	3.8 (0.73)	8.1 (0.32)	5.4 (1.54)
Site 2							
Fall	11.6	528 (177)	689 (181)	6.9 (2.55)	5.1 (1.46)	6.6 (3.19)	5.1 (1.61)
Winter	2.5	271 (50)	365 (66)	11.5 (6.15)	2.2 (0.40)	5.0 (0.43)	4.5 (1.01)
Spring	6.3	740 (450)	1,747 (405)	2.4 (0.15)	15.9 (7.13)	11.4 (2.23)	9.2 (2.22)
Summer	14.4	398 (75)	1,851 (304)	22.6 (13.25)	9.8 (3.02)	37.0 (24.32)	21.4 (13.41)

TABLE 3.—Pearson product moment correlations between the values for macroinvertebrate drift, rainbow trout gut fullness, temperature, and drift  $\times$  temperature (T30) values.

Variable	DDD	ODD	DDV	ODV	DGV	OGV	T30	DDD $\times$ T30	ODD $\times$ T30	DDV $\times$ T30
Daytime drift density (DDD)										
Overall drift density (ODD)	0.913									
Daytime drift volume (DDV)	0.545	0.479								
Overall drift volume (ODV)	0.710	0.872	0.181							
Daytime gut Volume (DGV)	0.739	0.732	0.808	0.446						
Overall gut volume (OGV)	0.751	0.780	0.793	0.522	0.994					
T30	0.759	0.481	0.273	0.305	0.478	0.440				
DDD $\times$ T30	0.938	0.755	0.617	0.472	0.794	0.771	0.869			
ODD $\times$ T30	0.955	0.886	0.669	0.611	0.889	0.889	0.724	0.956		
DDV $\times$ T30	0.726	0.618	0.906	0.325	0.934	0.911	0.583	0.835	0.859	
ODV $\times$ T30	0.924	0.888	0.503	0.831	0.735	0.760	0.711	0.854	0.891	0.725

about 90% of the variation in the value of these coefficients was associated with variation in  $D \times T$ . Neither of the length-weight regression coefficients were associated with site after we adjusted for  $D \times T$  (ANCOVA:  $F$ -test,  $df = 1, 5$ ;  $P > 0.89$ ), suggesting that variation in condition was not a function of unmeasured site variables.

Inclusion of other terms in the regression models did not result in better fits. Daytime drift density alone explained 82% of the variation in the slope and 84% of the variation in the intercept of the length-weight relationship but was always non-significant in the presence of  $D \times T$  and dropped from the model if a stepwise regression procedure was used. Regressions based on daytime drift volume alone or the product of daytime drift volume  $\times$  T30 also explained less variation than regres-

sions based on drift density and  $D \times T$  ( $r^2 =$  about 0.45 and 0.70). Temperature (T30) alone was associated with about 50% of the variation in both coefficients. When used alone, overall (day + night) drift estimates explained less variation in rainbow trout length-weight coefficients than their corresponding daytime drift estimates (e.g.,  $r^2 =$  0.82, 0.61, 0.44, and 0.24 for daytime drift density, overall drift density, daytime drift volume, and overall drift volume, respectively). However, drift  $\times$  T30 products based on daytime and overall drift estimates gave nearly identical  $r^2$  values. For the sake of brevity, we have not included all of the output from these regression analyses, but they can be calculated from data in Table 2 or obtained from the authors.

Results of the length-specific weight regressions

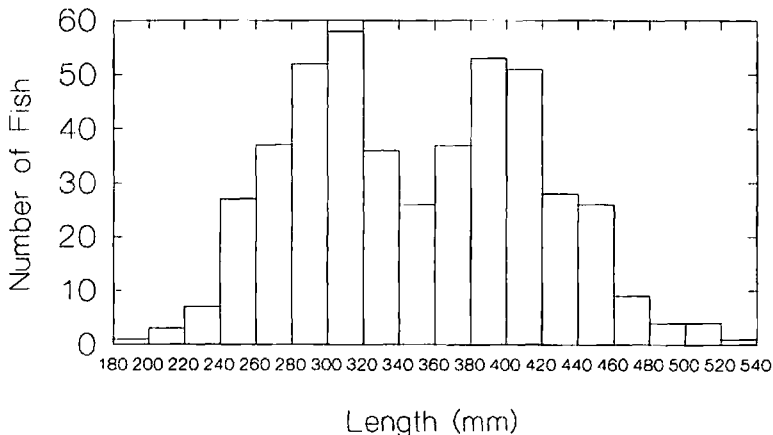


FIGURE 2.—Length distribution of 478 rainbow trout collected during the study.

TABLE 4.—Variation among sites and seasons in values of the coefficients describing the logarithmic ( $\log_{10}$ ) form of the length–weight relationship (text equation 3) for rainbow trout in the Green River.

Site and season	<i>N</i>	Intercept		Slope		<i>r</i> <sup>2</sup>
		log <i>a</i>	SE	<i>b</i>	SE	
Site 1						
Fall	58	−4.95	0.223	3.00	0.088	0.954
Winter	53	−5.28	0.119	3.11	0.047	0.988
Spring	61	−5.33	0.193	3.15	0.076	0.967
Summer	70	−4.74	0.127	2.92	0.050	0.980
Site 2						
Fall	58	−5.20	0.115	3.11	0.046	0.988
Winter	43	−5.22	0.176	3.10	0.069	0.980
Spring	56	−4.96	0.219	3.01	0.085	0.958
Summer	61	−4.14	0.105	2.70	0.041	0.986

showed that weight at length linearly increased with increasing values of  $D \times T$  for some, but not all lengths (Table 5), and  $D \times T$  explained a significant, usually high amount of variation in weight at length for rainbow trout between 200 and 350 mm long. Inclusion or use of other variables in these analyses generated results essentially identical to those obtained for the length–weight coefficients. Rainbow trout weight at length was significantly related to some drift measures when considered alone, but  $D \times T$  products always explained more variation in weight at length than did drift alone, and  $D \times T$  explained as much or more variation than products based on the other drift estimates.

Our analyses revealed that one of the data points exerted high leverage in these regression analyses (Figure 4). We therefore reanalyzed the data after excluding this observation (Table 5). Exclusion of the outlier modestly reduced the amount of variation in rainbow trout condition associated with  $D \times T$ , but exclusion did not significantly change the value of the regression coefficient  $b$  ( $P > 0.1$ ) with the exception of the coefficient for W200 ( $P < 0.04$ ). We therefore decided to base interpretations and future analyses of these data on all eight observations.

The magnitude of variation in condition was size-dependent. Weight of 200-mm fish varied by 57% across the observed gradients in temperature and drift density, that of 300-mm fish by 32%, and that by 400-mm fish by 18%. Some, although not all, of this variation was associated with the response of different sized fish to the food–temperature gradient. The slope of the weight at length versus  $D \times T$  relationship (see Figure 4) was a curvilinear function of fish length (Figure 5; see also values of  $b$  in Table 5). Slopes were highest for

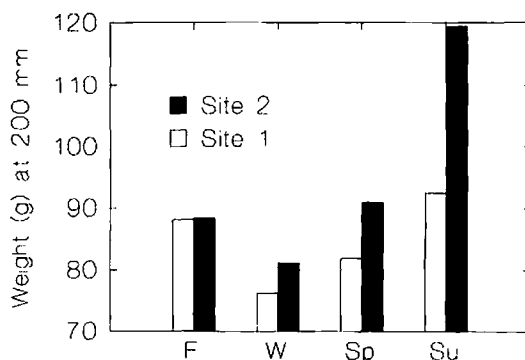


FIGURE 3.—Variation among seasons and sites in estimated weight of a 200-mm-long rainbow trout. Abbreviations are F = fall, W = winter, Sp = spring, and Su = summer.

375-mm rainbow trout and were lower for smaller and larger fish. In addition, as fish size increased, the regression models explained less of the variation in weight at length. The models accounted for about 90% of the variation in weight of 200-mm fish, only about 40% of variation in weight of 400-mm fish, and none of the variation in weight for 500-mm fish.

Output from the bioenergetic model also de-

TABLE 5.—Regression statistics describing the relations between the intercept and slope coefficients of the log weight–log length relation (W–L) and estimated weights at length of rainbow trout versus the product of daytime drift density  $\times$  T30 ( $D \times T$ ).

Dependent variable <sup>a</sup>	<i>D</i> × <i>T</i>		<i>r</i> <sup>2</sup>	<i>P</i>
	Intercept ( <i>a</i> )	Slope ( <i>b</i> )		
Outlier included ( <i>N</i> = 8)				
Intercept (W–L)	– 5.358	0.0000674	0.910	0.000
Slope (W–L)	3.151	– 0.0000249	0.890	0.000
Length-specific weight				
W200	77.140	0.00225	0.912	0.000
W300	279.390	0.00415	0.821	0.002
W350	455.043	0.00461	0.673	0.013
W400	693.909	0.00438	0.416	0.084
W500	1,402.982	0.00062	0.003	0.903
Outlier excluded ( <i>N</i> = 7)				
Intercept (W–L)	– 5.308	0.0000519	0.752	0.011
Slope (W–L)	3.133	– 0.0000192	0.693	0.020
Length-specific weight				
W200	79.528	0.00150	0.823	0.005
W300	283.483	0.00286	0.508	0.072
W350	459.524	0.00320	0.284	0.218
W400	698.225	0.00302	0.112	0.463
W500	1,404.580	0.00012	0.000	0.990

<sup>a</sup> Weight is denoted by W; number following a W is total fish length.

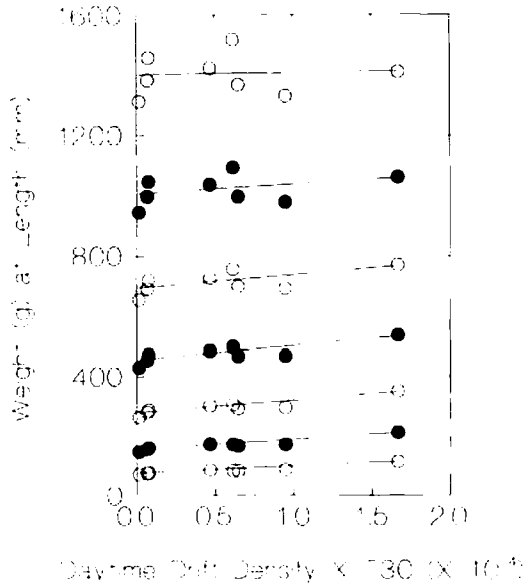


FIGURE 4.—Relations between weight at length for 200, 250, 300, 350, 400, 450, and 500-mm-long rainbow trout and the product of daytime drift density (milliliters of invertebrates per 100 m<sup>3</sup>) and temperature (mean temperature at each site during the 30 d before each sampling date). Note the apparent outlier at 16,690 drift  $\times$  temperature units. (Open and closed circles are used for clarity only.) Lines were fitted by regression, and most slopes are given in Table 5. The effect of excluding the apparent outlier is also given in Table 5.

scribed a food-temperature interaction similar, although not identical, to our observations (Figure 6). The fit between empirical and modeled results was closest for small rainbow trout and increasingly diverged as individual size increased. Our data also indicated that highest condition occurred at 14.5°C, the highest mean monthly temperature encountered, whereas the model predicted maximum growth should occur between 11 and 13°C. Because our data showed no evidence that condition declined over any part of the temperature gradient encountered, the actual summer temperature optimum for rainbow trout in the Green River at high levels of food is probably warmer than 15°C.

### Discussion

Several studies have shown that stream trout abundance or growth is correlated with food availability. Food limitation has been inferred for stream salmonids from several geographical areas including the Pacific Northwest (Murphy et al. 1981; Hawkins et al. 1983; Wilzbach 1985; Baker

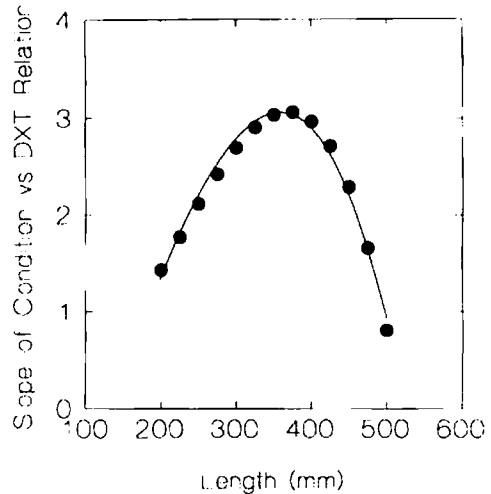


FIGURE 5.—Relations between rainbow trout length and slope of the weight at length versus the daytime drift density  $\times$  temperature ( $D \times T$ ) relationship. Slopes were calculated at 25-mm intervals. The curve was fitted by computer with a distance-weighted least-squares algorithm (Wilkinson 1992).

1989). Intermountain West (Binns and Eiserman 1979), Appalachia (Cada et al. 1987; Ensign et al. 1990), northeastern North America (Bowlby and Roff 1986a, 1986b), and Alaska (Hughes and Dill 1990). The relations between rainbow trout weight at length, drift abundance, gut volumes, and temperature that we observed in the Green River also imply that growth of rainbow trout here was food-limited, although, as expected, the limitation was mediated through an interaction with temperature. This is the type of interaction that Brett et al. (1969) and Elliott (1976) described from laboratory studies. Their analyses showed that (1) the effect of varying food quantity was greatest at the temperature optimal for growth, (2) the effect of varying temperature was small under conditions of low food and increased as amount of food available to individual fish increased, and (3) small fish were most sensitive to variation in both food and temperature.

Because quantifying individual rainbow trout growth was beyond the scope of this study, we could not directly evaluate how growth varied with differences in food and temperature. However, we believe change in condition is an expression of growth and thus interpret our data to imply that growth by rainbow trout in the Green River was jointly limited by food availability and temperature. This interpretation is intuitively sensible, considering that the thermal optimum for growth



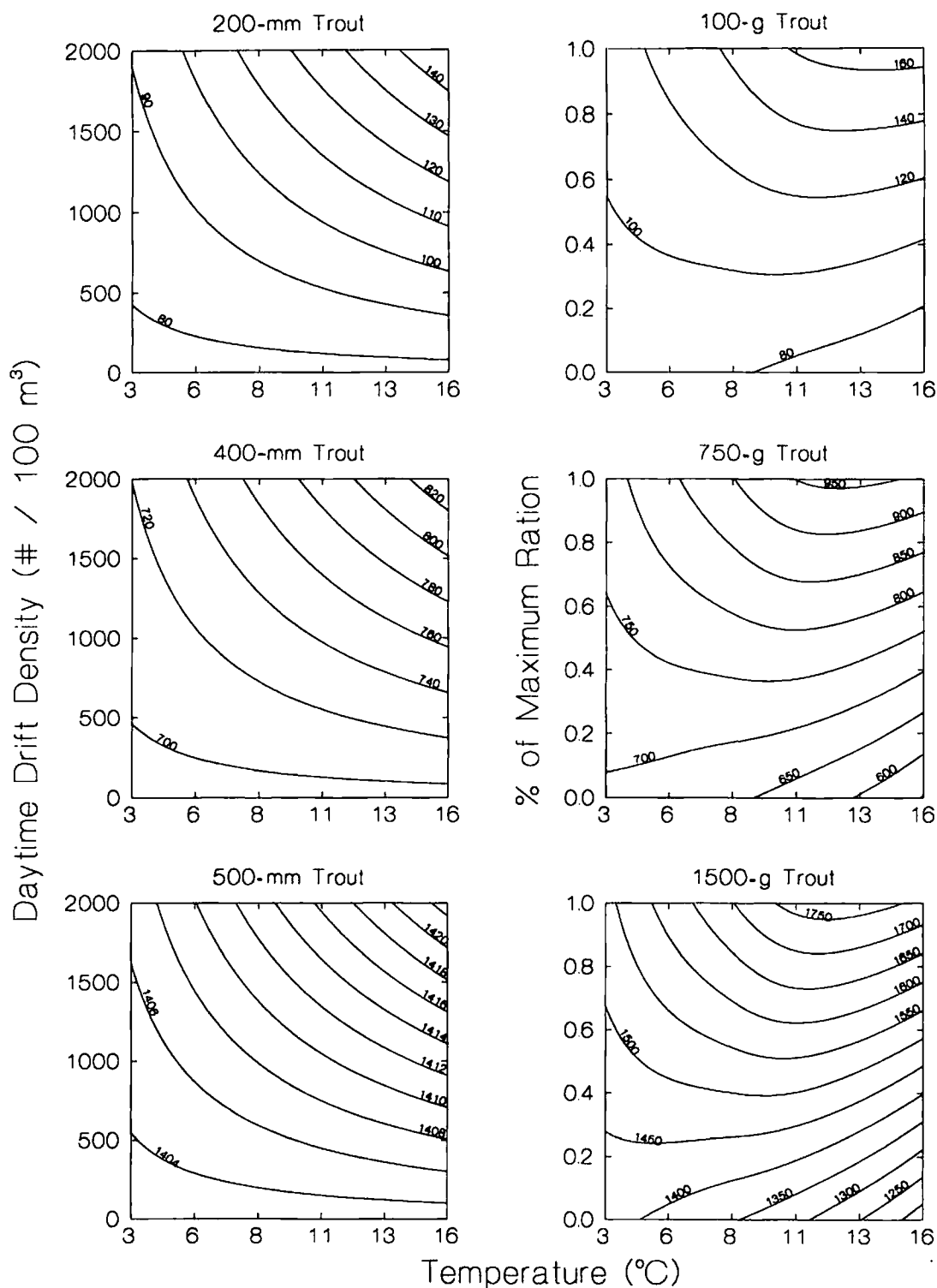


FIGURE 6.—Contour surfaces describing variation in observed (left column) and modeled (right column) rainbow trout weight as a function of fish size, food (daytime drift density or % maximum ration), and temperature. The left column describes variation among sites and seasons in weight at length for 200, 400, and 500-mm rainbow

of rainbow trout in the laboratory is about 17°C (Hokanson et al. 1977), and that fish in our study experienced an 11°C range in mean monthly temperature and a greater than 17-fold range of drift abundance across sites and seasons. However, unlike the pattern of maximum possible growth at temperature observed by Elliott (1976) for young brown trout in the wild (i.e., no evidence for food limitation), condition of rainbow trout in the Green River appeared to be lower than possible for the temperatures encountered. Considering that condition was related to drift abundance alone but not temperature alone, we infer that rainbow trout growth was largely limited by food availability.

The observed size-dependency in the response of condition across the food-temperature gradient may be related to several factors. Very large fish (i.e., those near 500 mm) might be expected to show little change in condition because the absolute accrual of mass is small compared to their total weight. Furthermore, large fish may allocate more energy to reproduction than somatic growth and thereby exhibit little, if any, change in body mass.

The relative growth rates of most species decrease as individual size increases. However, in the Green River, medium-sized rainbow trout (300–350 mm) showed the strongest response to changes in the food-temperature gradient. The condition of small fish (about 200 mm) may have changed little in response to this gradient because they had been recently stocked and thus may have been inefficient feeders on natural prey and inept at selecting microhabitats that minimized maintenance costs. Newly stocked fish may have also spent much of their time avoiding predators. Predator avoidance may have been especially problematic at site 2, where brown trout were more abundant. The greater variation in condition observed in medium-sized rainbow trout may be the result of progressively improved foraging, habitat selection, and predator avoidance behaviors. Alternatively, if size-structured dominance hierarchies exist in the Green River, smaller fish may be competitively excluded from the most profitable for-

aging locations by larger fish. The latter hypothesis would explain why so much of the variation in condition of small fish was related to the food-temperature gradient (>90%) and why the slope of the condition versus food  $\times$  temperature product was low.

It is not clear whether the discrepancies between observed and modeled data resulted from inaccuracies in field measurements, small sample size, or inaccurate assumptions regarding parameter values on which output from the bioenergetics model depends. Considering that empirical and modeled results diverged with increasing individual size, we suspect one or more size-dependent metabolic parameters may need refinement in the model. Although the observed differences were not trivial, the degree of correspondence was close enough to suggest that refined models may accurately describe the growth of wild trout. Attempts to reconcile field and model results should improve our understanding of the way food and temperature interact to influence growth. One thing that seems clear from these comparisons is that the actual temperature optimum for rainbow trout in the Green River is probably closer to that reported by Hokanson et al. (1977) than that predicted by the bioenergetic model. If true, dam managers could potentially increase the growth of all size-classes of rainbow trout by releasing warmer water. This conclusion also has important implications for management of several endangered species of nongame fish, all of which require higher temperatures than exist within the study reach.

We believe the predictive power of current stream habitat models might be improved by incorporating variables that describe how food availability and water temperature influence trout production under different habitat conditions. A few investigators have examined how drift varies with flow (e.g., Minshall and Winger 1968; Brooker and Hemsworth 1978; White and Wade 1980; Irvine 1985), but no general quantitative relationships have emerged. Future research should focus on studies designed to determine the environmental conditions under which stream fish production is

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trout. The right column describes predicted changes in weight (g) over a 30-d period from the initial weight shown above each diagram. Initial trout weights in the left column approximately correspond to initial weights in the right column. We generated contours for observed weight at length by plotting the regression equations in Table 5 that describe the relations between weight at length and the product of daytime drift density and mean temperature. Model contours were generated from weights predicted for 25 combinations of ration and temperature. In both columns, the numbers of contour lines are arbitrary and were simply chosen for visual clarity.

food-limited. Such research should focus on quantifying spatial and temporal differences in temperature and food availability, ascertaining the causes of those differences, and determining whether flow changes cause predictable variation in drift abundance.

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### References

- Allan, J. D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 184-192.
- Allan, J. D., and E. Russek. 1985. The quantification of stream drift. *Canadian Journal of Fisheries and Aquatic Sciences* 42:210-215.
- Armitage, P. D. 1978. Downstream changes in the composition, numbers and biomass of bottom fauna in the Tees below Cow Green Reservoir and in an unregulated tributary Maize Beck, in the first five years after impoundment. *Hydrobiologia* 58:145-156.
- Baker, A. 1989. Variation in trout abundance in relation to habitat quality in a recently disturbed stream: patterns at two spatial scales. Master's thesis. Utah State University, Logan.
- Binns, N. A., and F. M. Eiserman. 1979. Quantification of fluvial trout habitat in Wyoming. *Transactions of the American Fisheries Society* 108:215-228.
- Bisson, P. A. 1978. Diel food selection by two sizes of Rainbow trout (*Salmo gairdneri*) in an experimental stream. *Journal of the Fisheries Research Board of Canada* 35:971-975.
- Bowlby, J. N., and J. C. Roff. 1986a. Trophic structure in southern Ontario streams. *Ecology* 67:1670-1679.
- Bowlby, J. N., and J. C. Roff. 1986b. Trout biomass and habitat relationships in southern Ontario streams. *Transactions of the American Fisheries Society* 115:503-514.
- Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Research Board of Canada* 26:2363-2394.
- Brooker, M. P., and R. J. Hemsworth. 1978. The effect of the release of an artificial discharge of water on invertebrate drift in the River Wye, Wales. *Hydrobiologia* 59:155-163.
- Cada, G. F., J. M. Loar, and M. J. Sale. 1987. Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. *Transactions of the American Fisheries Society* 116:692-702.
- Cone, S. R. 1989. The need to reconsider the use of condition indices in fishery science. *Transactions of the American Fisheries Society* 118:510-514.
- Cone, R. C. 1990. Properties of relative weight and other condition indices. *Transactions of the American Fisheries Society* 119:1048-1058.
- Elliott, J. M. 1970. Diel changes in invertebrate drift and the food of trout (*Salmo trutta* L.). *Journal of Fish Biology* 2:161-165.
- Elliott, J. M. 1973. The food of brown and rainbow trout (*Salmo trutta* and *Salmo gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. *Oecologia* 12:329-347.
- Elliott, J. M. 1975a. The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. *Journal of Animal Ecology* 44:805-821.
- Elliott, J. M. 1975b. The growth rate of brown trout (*Salmo trutta* L.) fed on reduced rations. *Journal of Animal Ecology* 44:823-842.
- Elliott, J. M. 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *Journal of Animal Ecology* 45:923-948.
- Elliott, J. M. 1979. Energetics of freshwater teleosts. *Symposia of the Zoological Society of London* 44: 29-61.
- Ensign, W. E., R. J. Strange, and S. E. Moore. 1990. Summer food limitation reduces brook and rainbow trout biomass in a southern Appalachian stream. *Transactions of the American Fisheries Society* 119: 894-901.
- Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to energy gain. *Canadian Journal of Zoology* 62:441-451.
- From, J., and E. Rasmussen. 1984. A growth model, gastric evacuation, and body composition in rainbow trout, *Salmo gairdneri* Richardson, 1836. *Dana* 3:61-139.
- Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Riparian canopy and substrate composition interact to influence the abundance of salmonids, sculpins, and salamanders in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1173-1185.
- Hewett, S. W., and B. L. Johnson. 1992. Fish bioenergetics model 2. University of Wisconsin, Sea Grant Institute, Technical Report WIS-SG-92-250, Madison.
- Hokanson, K. E. F., C. F. Kleiner, and T. W. Thorsland. 1977. Effects of constant temperature and diel fluctuations on growth, mortality, and yield of juvenile rainbow trout, *Salmo gairdneri* (Richardson). *Journal of the Fisheries Research Board of Canada* 34: 639-648.
- Hughes, N. F., and L. M. Dill. 1990. Position choice

- by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2039–2048.
- Irvine, J. R. 1985. Effects of successive flow perturbations on stream invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1922–1927.
- Jenkins, T. M., C. R. Feldmeth, and G. V. Elliott. 1970. Feeding of rainbow trout (*Salmo gairdneri*) in relation to abundance of drifting invertebrates in a mountain stream. *Journal of the Fisheries Research Board of Canada* 27:2356–2361.
- Johnson, J. E., R. P. Kramer, E. Larson, and B. L. Bonebrake. 1987. Trout growth, harvest, survival, and microhabitat selection in the Green River, Utah, 1978–1982. Final Report, Flaming Gorge Tailwater Fisheries Investigations. Utah Division of Wildlife Resources Publication 87-13, Salt Lake City.
- Kimball, D. C., and W. T. Helm. 1971. A method of estimating fish stomach capacity. *Transactions of the American Fisheries Society* 100:572–575.
- Le Cren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology* 20:201–219.
- McNicol, R. E., E. Scherer, and E. J. Murkin. 1985. Quantitative field investigation of feeding and territorial behavior of young-of-the-year brook charr, *Salvelinus fontinalis*. *Environmental Biology of Fishes* 12:219–229.
- Metz, J. 1974. Die Invertebratendrift an der Oberfläche eines Voralpenflusses und Ihre Selektive Ausnutzung durch die Regenbogenforellen (*Salmo gairdneri*). *Oecologia* 14:247–267.
- Minshall, G. W., and P. V. Winger. 1968. The effect of reduction in stream flow on invertebrate drift. *Ecology* 49:580–582.
- Modde, T., D. A. Young, and D. Archer. 1991. Evaluation of factors influencing population characteristics and habitat utilization of trout in the Flaming Gorge tailwater, 1987–1989. Utah Division of Wildlife Resources, Publication 91-10, Salt Lake City.
- Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. *Transactions of the American Fisheries Society* 110:469–478.
- Pearson, W. D. 1967. Distribution of macroinvertebrates in the Green River below Flaming Gorge Dam, 1963–1965. Master's thesis. Utah State University, Logan.
- Platts, W. S., W. Meghahan, and W. G. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. U.S. Forest Service General Technical Report INT-138.
- Slaney, P. A., and T. G. Northcote. 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. *Journal of the Fisheries Board of Canada* 31:1201–1209.
- Ward, J. V. 1974. A temperature-stressed stream ecosystem below a hypolimnial release mountain reservoir. *Archiv für Hydrobiologie* 74:247–275.
- Wetzel, R. G., and G. E. Likens. 1990. Limnological analyses, 2nd edition. Springer-Verlag, New York.
- White, R. G., and D. T. Wade. 1980. A study of fish and aquatic macroinvertebrate fauna in the South Fork Boise River below Anderson Ranch Dam with emphasis on effects of fluctuating flows. University of Idaho, College of Forestry, Wildlife, and Range Sciences, Technical Completion Report 14-06-100-9220, Moscow.
- Wilkinson, L. 1992. SYSTAT for Windows: statistics, version 5 edition. SYSTAT, Inc., Evanston, Illinois.
- Wilzbach, M. A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). *Canadian Journal of Fisheries and Aquatic Sciences* 42:1668–1672.

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