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Determination of Population-limiting Critical Salmonid Habitats in Colorado Streams Using the Physical Habitat Simulation System

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ABSTRACT: We used the Instream Flow Incremental Methodology (IFIM) and Physical Habitat Simulation system (PHABSIM) to investigate the influence of stream discharge and the concomitant variation in habitat on wild rainbow (*Oncorhynchus mykiss*) and brown (*Salmo trutta*) trout populations in 11 Colorado streams. We identified critical salmonid habitat limitations on 10 of the 11 streams studied over a 13-year period. The 2-4-week-old fry, egg incubation, and spawning life stages were most sensitive to critical habitat "bottlenecks." Linear regression analyses revealed statistically significant correlations ($P \leq 0.05$) between weighted usable area (WUA), an index of physical habitat quality and quantity (determined using PHABSIM), and density (n/ha) of age-1 or -2 rainbow and brown trout in 10 of 11 streams studied. Correlations between WUA (based on mean monthly flow) and density were superior in both accuracy and precision in properly identifying population-limiting events compared to correlations between mean monthly stream discharge (during the critical time period) and trout density.

KEY WORDS: Brown trout, habitat limitations, instream flow, rainbow trout, IFIM, PHABSIM

INTRODUCTION

Biologists have attempted modeling stream habitat for decades (Fausch et al. 1988). However, few stream habitat models have generated more controversy than the Instream Flow Incremental Methodology (IFIM). In particular, the Physical Habitat Simulation system (PHABSIM) has been a focus of the debate. An early paper by Orth and Maughan (1982) discussing the relative merits of PHABSIM focused the attention. Subsequent papers either criticized the IFIM approach (Mathur et al. 1985, 1986; Shirvell 1986, 1989; Scott and

Shirvell 1987), or supported it (Anderson and Nehring 1985; Mosley and Jowett 1985; Orth and Maughan 1986; Irvine et al. 1987). Despite the controversy, the IFIM is still used for stream habitat studies in North America (Reiser et al. 1989) and other parts of the world (Jowett 1992).

The IFIM, developed by the U.S. Fish and Wildlife Service in Fort Collins, Colorado, uses hydraulic simulation techniques to predict changes in water depth, velocity, substrate, and cover on an area basis at different levels of streamflow.

Model output, when fed into the PHABSIM, transforms hydraulic information at various flows into units of physical habitat called weighted usable area (WUA). Quantification of WUA is usually based on fish habitat preferences for water depth and velocity, substrate, and cover. However, other factors (e.g., water temperature, water quality, suspended silt) can be incorporated. Field techniques, theory, and data handling have been described in various publications (Bovee and Cochnauer 1977; Bovee 1978, 1982; Bovee and Milhous 1978; Milhous et al. 1984).

Although PHABSIM is a complex modeling system (Jowett 1992), we believe it is unique among habitat models in its ability to convert stream hydraulic data (measures of energy gain and loss) into habitat units for a variety of fish species and life stages. Several studies have shown that trout innately select feeding and resting positions to maximize energy gain (Jenkins 1969; Bachman 1984; Fausch 1984). They indicate that trout feeding and resting site selection is based primarily on depth, water velocity,

and proximity to cover. Ottaway and Clarke (1981) and Ottaway and Forrest (1983) showed that water velocity (a measure of energy) is an important factor negatively affecting salmonid fry survival.

Although the IFIM concept has existed since the 1970's (Stalnaker and Arnette 1976), we believe that the study by Jowett (1992) is the only published account of a rigorous attempt at field validation of the PHABSIM models on many streams. The overall goal of our study was to measure trout population response to temporal and spatial variation in stream habitat (WUA) as quantified by the PHABSIM models. Specific study objectives were to: (1) determine if mean monthly discharge (MMD) or trout habitat units (WUA) were more reliable indicators of trout density over long periods of time (5 years or more) for a wide range of streams and flow conditions (Table 1), and (2) determine if the PHABSIM models could reveal at what life stage habitat perturbations were most limiting to stream trout populations in Colorado.

METHODS

Study Areas

Eleven PHABSIM study sites and 21 population estimation study areas were located on 11 streams of varying size, discharge, and elevations throughout the mountainous regions of Colorado (Figure 1, Table 1). Impoundments, diversions, and flow augmentation (in some instances) affected study stream discharge hydrographs to some degree.

Species composition and diversity varied among study streams. The salmonid populations of the Arkansas, Blue, Rio Grande, South Fork of the Rio Grande, St. Vrain, and Taylor rivers were allopatric brown trout (*Salmo trutta*). Sympatric populations of rainbow (*Oncorhynchus mykiss*) and brown trout comprised the salmonid community in the Cache la Poudre, Colorado, Fryingpan, Gunnison, and South Platte rivers. Salmonids accounted for most of the fish biomass, and species diversity was low in all study streams. Nongame species of the families Catostomidae, Cyprinidae, and Cottidae accounted for most of the remaining density and biomass.

Study streams contained from two to six nongame species, including white (*Catostomus commersoni*), longnose (*C. catostomus*), bluehead (*C. discobolus*), and flannelmouth (*C. latipinnis*) suckers, longnose (*Rhinichthys cataractae*) and speckled (*R. osculus*) dace, and mottled sculpin (*Cottus bairdi*).

On most streams (such as the Arkansas River), the PHABSIM study site was contained within (but not coincident to) a population study reach. The PHABSIM study site and population study reach were coincident on the Fryingpan, South Platte, and St. Vrain rivers. On the Cache la Poudre, Colorado, Gunnison, Rio Grande, and South Fork of the Rio Grande rivers, we used a single PHABSIM study site (contiguous with one population study area) to characterize habitat (WUA) availability for two to five population study reaches. In some instances, PHABSIM sites and population study reaches were separated by 30–50 km of river. However, channel configuration and geomorphology were similar within study streams, and flow regime among population study sites was highly colinear within years. The PHABSIM study

TABLE 1
Study stream names, trout population study sites, elevation, and discharge characteristics.

River	Time period (years)	No. population study sites	Study site elev. (m)	Discharge (m ³ /sec)		
				Mean annual	Minimum monthly	Maximum monthly
Arkansas	1979–1985	1	2,098	10.9	6.63	111
Blue	1980–1984	3	2,671	5.87	0.88	51.4
Cache la Poudre	1960–1986	5	1,591	11.1	0.48	135
Colorado	1979–1986	2	2,338	22.8	2.64	97.5
Fryingpan	1978–1986	6	2,278	5.38	0.96	26.9
Gunnison	1960–1986	2	1,585	39.7	6.55	227
Rio Grande	1980–1991	3	2,433	25.9	4.70	160
South Fork of Rio Grande	1976–1982	3	2,507	6.06	0.39	49.5
St. Vrain	1980–1984	2	1,613	3.66	0.32	24.9
South Platte	1977–1986	3	2,015	4.79	0.68	27.9
Taylor	1972–1986 ^a	3	2,796	5.67	1.36	21.5

^a Includes data from 11 of 15 years.

sites on the Blue and Taylor rivers were separate from the trout population study areas.

With the exception of the Taylor River, no flow control or modification of stream discharge was undertaken to facilitate habitat alteration or trout population response as part of this study. On the Taylor River, discharge was tightly controlled by a large headwater impoundment. Water stored in Taylor Park Reservoir was released downstream for hydropower, irrigation, industrial, and domestic water needs. Before 1976, the discharge was maintained at unusually high levels (11–17 m³/sec) from October to mid-December, vacating storage capacity to facilitate capture of spring run-off water the next year. Once adequate reservoir storage space had been vacated, reservoir discharge was reduced to 0.3–1.4 m³/sec. A study by Burkhard tested the hypothesis that this distorted fall-winter discharge pattern was negatively affecting the Taylor River brown trout population (W. T. Burkhard, unpublished data).

Spring and fall trout population estimates were completed at five stations on the Taylor River in 1974 and 1975 under the high fall-low winter discharge regime. Beginning in 1976, fall-winter discharge patterns were stabilized before the onset of brown trout spawning. A 3-year waiting period (1976–1978) allowed the trout population to restabilize under the new flow

regime. Trout population estimation procedures were again initiated from 1979 through 1982 to evaluate the effect of fall-winter flow stabilization on brown trout population density. Although the flow modification study began before our investigation, the results are germane and are included here.

Study Design and Methodology

Field validation of the PHABSIM model involved four phases. First, we set up PHABSIM study sites on 11 streams (Table 1, Figure 1) between 1978 and 1985. Six to ten transects were used to characterize each study site, which varied in length from 100 m to more than 700 m. Field data measurements (water velocity, depth, substrate type, and discharge measurements) were taken at least three different times at each site over one hydrologic cycle as outlined by Bovee and Milhous (1978), and entered into the PHABSIM model for calibration.

Second, we ran calibrated data decks through the PHABSIM model using Habitat Suitability Criteria (HSC) curves for rainbow and brown trout taken from Bovee (1978) and Raleigh et al. (1986) (except for the fry life stage) to produce WUA values by species and life stage for the appropriate range of flows for each study stream. Field observations indicated that the depth and velocity preference curves for newly

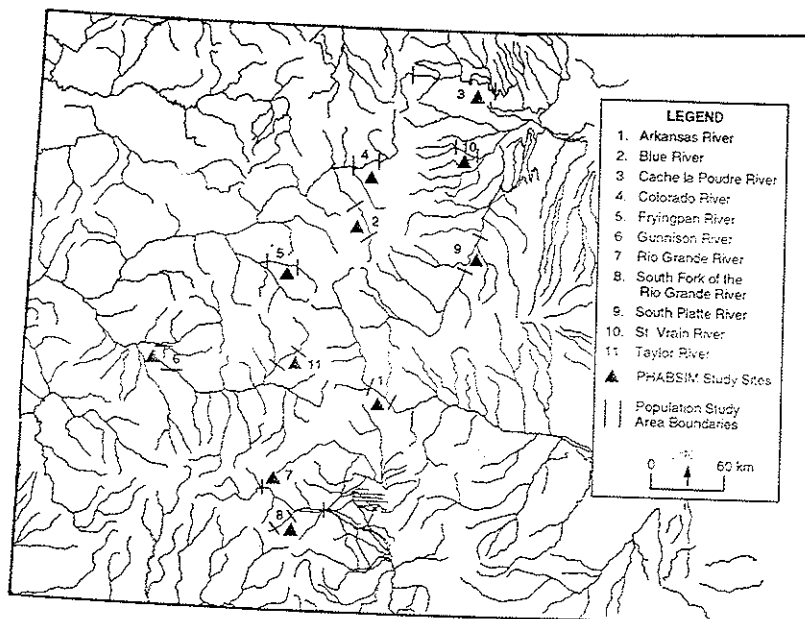


FIGURE 1. Drainage map of the mountainous region of Colorado. Numbered triangles denote the approximate location of the Physical Habitat Simulation (PHABSIM) study sites on each stream. Vertical bars denote the approximate boundaries of the trout population estimation study areas.

emerged rainbow and brown trout fry should be more narrowly defined than those shown in Bovee (1978). Therefore, we developed depth and velocity HSC curves for 2-4-week-old fry based on hab-

TABLE 2
Normalized (0.0-1.0) frequency distribution of depth and velocity preferences for 2-4-week-old rainbow and brown trout fry.

Depth (cm)	Normalized frequency	Velocity (cm/sec)	Normalized frequency
0.00	0.00	0.00	1.00
3.05	0.40	3.05	0.45
6.10	1.00	6.10	0.37
9.15	1.00	9.15	0.28
12.19	1.00	12.19	0.10
15.24	1.00	15.24	0.04
18.29	0.30	18.29	0.03
21.34	0.20	21.34	0.02
24.38	0.14	24.38	0.01
27.43	0.04	27.43	0.00
30.48	0.00	30.48	0.00

itat preferences of more than 350 rainbow and brown trout fry observed over two field seasons (Table 2). For 2-4-week-old fry, all substrates were rated at unity. Our depth and velocity HSC curves for trout fry were very similar to those developed in Montana by Sando (1981). In our study, any use of the term "fry WUA" refers to the habitat of 2-4-week-old trout fry. Weighted usable area for all life stages was calculated using depth, velocity, and substrate preferences. We classified substrate using the modified Brusven Index reported by Bovee (1982).

Third, trout population data (species density, biomass, and population age structure) were collected for 5 or more years on each study stream in the fall and occasionally in the spring. This data base was the source for the age-specific estimates of rainbow and brown trout density, the dependent variables to be paired with the independent variables of MMD and WUA.

Fourth, simple linear regression analyses and Pearson correlation coefficients (r)

TABLE 3
Approximate time and duration of spawning, and the critical early developmental life stages for brown and rainbow trout in 11 Physical Habitat Simulation (PHABSIM) study streams.

River	Species	Time period (month/day)			
		Adult spawning	Egg incubation	Egg hatching	Fry emergence
Arkansas	Brown	10/15-11/15	10/15-4/1	3/1-5/1	4/1-6/1
Blue	Brown	10/15-11/15	10/15-6/1	4/1-6/1	5/15-7/1
Cache la Poudre	Brown	10/15-11/15	10/15-6/1	4/1-6/1	5/15-7/1
Cache la Poudre	Rainbow	4/15-5/30	4/15-7/15	6/15-7/15	7/1-8/1
Colorado	Brown	10/15-11/15	10/15-4/1	4/1-6/1	5/15-6/15
Colorado	Rainbow	4/15-4/30	4/15-6/15	6/1-7/1	6/15-7/15
Fringingan	Brown	10/15-11/15	10/15-5/1	4/1-6/1	5/15-6/15
Fringingan	Rainbow	4/1-5/1	4/1-6/15	6/1-7/1	6/15-7/15
Gunnison	Brown	10/15-11/15	10/15-4/1	3/15-5/15	5/1-6/15
Gunnison	Rainbow	4/1-5/1	4/1-6/15	6/1-7/1	6/15-7/15
Rio Grande	Brown	10/15-11/15	10/15-5/1	4/1-6/1	5/15-6/15
South Fork of Rio Grande	Brown	10/15-11/15	10/15-6/1	5/1-7/1	6/1-7/15
South Platte	Brown	10/15-11/15	10/15-5/1	4/1-6/1	5/1-6/15
South Platte	Rainbow	4/1-5/15	4/1-6/1	6/1-7/1	6/15-7/15
St. Vrain	Brown	10/15-11/15	10/15-5/1	4/1-6/1	5/15-7/1
Taylor	Brown	10/15-10/30	10/15-5/1	4/1-6/1	5/15-7/1

were used to check for linear association between dependent (trout population density) and independent (WUA and MMD) variables over the time span for which trout population data and discharge records were available. For consistency, and to limit heterogeneity of the data, we used natural logarithmic transformations of x and y variables. The Statistical Analysis System (SAS) was used for all analyses (SAS Institute 1985a, 1985b). All references to statistical significance refer to the 5% level or less.

During the time of fry emergence, age-1 and -2 trout population density (n/ha) and trout fry WUA were positively correlated and density and mean monthly discharge (MMD) were negatively correlated. Therefore, we used a one-tailed t -test to determine the level of significance. For each study stream, we used U.S. Geological Survey monthly gaging data to determine MMD and the corresponding habitat units (WUA).

Data sets for regression analysis were created in the following manner: for the early life stages (spawning, egg incubation, hatching, and fry) we paired age-specific (age-1 or -2) trout density (the dependent variable) in year n with MMD or WUA (independent variables) for a life stage-specific critical period (in year $n-1$ or $n-2$), correspondent with the dependent

variable age factor. Similar pairings for all years that trout population density data were available created a data set for regression analysis. For the adult life stages, the dependent variable (trout density \geq age 2) in year n was paired with the independent variables in year n . Independent variables for the adult life stage were average summer (April-October) MMD or WUA.

For the fry life stage, significant correlations were considered valid only when corroborated by time (month) and site-specific collections of newly emerged (20-40-mm-total length) trout fry. Significant correlations between trout density and fry WUA or MMD that were not synchronous with the fry emergence period were considered spurious. However, we report spurious significant correlations to determine whether WUA or MMD more accurately and precisely defined the critical habitat "bottlenecks."

The approximate times and durations of the four early developmental life stages for rainbow and brown trout in the 11 study streams are given in Table 3. We collected rainbow and brown trout fry for all study streams to document the fry emergence period. At a minimum, each study stream was visited monthly between 1 April and 15 July 1988 to document the time of fry emer-

gence. On some streams fry sampling was conducted over several years. When present, at least 10 fry were collected. A stereo zoom binocular microscope was used to identify trout fry (Martinez 1984) and then measure total length (TL) to the nearest millimeter. The date of collection, number of fry (by species), mean size (mm TL), and size range of fry in the sample(s) were used to estimate critical time periods for each species and stream.

Because each stream trout population was evaluated for 5–11 years, each regression analysis has a minimum of five data points. Exclusive of the adult life stage, correlations were usually calculated between age-1 density and WUA (or MMD) because the effects of angler harvest were negligible, but the fish were large enough (120–200 mm TL) to be efficiently sampled by electrofishing. In a few streams with slow trout growth rates, third summer (age-2) trout density was used because these fish were still below the minimum size (200 mm TL) generally harvested by anglers.

Population estimation procedures and electrofishing techniques varied among streams but were constant within streams and study sites between years. We used two pass removal estimators (Seber and LeCren 1967) on small streams < 15-m average width. Station length ranged from 183 to 335 m among streams. Elapsed time between passes was usually 1–2 hr.

On streams averaging 15–29 m wide the Petersen (mark-and-recapture) method was employed. Study station length ranged

from 183 to 355 m. Twenty-four- to 48-hr time elapse between passes allowed captured fish to recover normal body function (Schreck et al. 1976; Mesa and Schreck 1989) and redistribute within the study site.

On large unwadeable rivers (≥ 30 -m average width) we used a Jon boat for electrofishing. Populations were estimated using the Schnabel (multiple mark-and-recapture) method. Sample stations ranged from 3 to 11 km in length, and three or four mark-and-recapture runs were required to obtain reliable population estimates (Robson and Regier 1968). A minimum of 72 hr was allowed between electrofishing passes. Nine to 14 days were required to complete the Schnabel population estimates.

Due to size selectivity of the electrofishing equipment, population estimates were computed for each 5-cm size group. All trout captured were measured to the nearest centimeter. Scale samples (five trout per species per centimeter length group at each study site) were aged each year. We used length and age distributions to divide the population estimate into age-specific density estimates; for example, the number of age-1 trout/ha. Density estimates by species for each study stream for a series of years were then paired with the mean monthly WUA and MMD for the critical time periods and tested using linear regression analysis. Because data sets for all study streams have been reported previously (Nehring 1988), they will not be included here.

RESULTS

General Results

Across all study streams and sites, trout density was significantly correlated with habitat (WUA) or discharge (MMD) in 112 instances (Table 4). In 77 instances (Table 4), we found the timing, magnitude, and variation in fry WUA or MMD during the fry emergence period to be significant factors constraining rainbow and brown trout recruitment among 10 of 11 study streams and 20 of 22 study sites. Fluctuations in spawning habitat or discharge (Δ WUA, Δ MMD) between egg deposition and hatching during the winter months were identified as critical habitat limitations at

three sites. Spawning habitat (WUA) or discharge (MMD) limited trout density at two sites (Table 4). We found a positive association between brown trout density and January incubation discharge (MMD) and habitat (WUA) at two of three study sites on the Taylor River. On the Colorado River, brown trout hatching flows (April MMD) were identified as a habitat "bottleneck" at one study site (Table 4). There were 19 instances of spurious correlation between trout density and fry WUA or discharge (during the fry emergence) that were not validated by on-site fry collections (Table 4).

We found no significant correlations be-

tween trout density and spawning flows (MMD), spawning WUA, average summer adult WUA, or average summer discharge for the Arkansas, Blue, Cache la Poudre, Fryingpan, Gunnison, Rio Grande, South Fork of the Rio Grande, South Platte, and St. Vrain rivers. We found no significant correlations between trout density and average summer adult WUA or discharge for the Colorado and Taylor rivers (Table 4). The Fryingpan River was the only study stream where mitigating factors and circumstances precluded finding significant relationships between rainbow or brown trout density and habitat (WUA) or discharge (Nehring 1991).

Compared to the density and MMD correlations, the correlations between trout density and WUA resulted in more significant correlations, fewer instances of non-significance where the parallel correlation was significant, more instances of stronger correlation, and fewer spurious correlations (Table 5). These results indicate that, compared to MMD, WUA more accurately and precisely identified periods of physical habitat limitations to trout density. Examination of the results for individual streams demonstrates the utility and adaptability of the PHABSIM methodology for elucidating the trout population response to flow-induced variations in physical habitat (WUA).

River-specific Results

Arkansas River. During 6 years of study, age-1 brown trout density was negatively correlated with July mean monthly discharge (MMD) and age-2 density was negatively correlated with June MMD (Table 4). Brown trout fry WUA was not correlated with density. However, by averaging fry WUA (and MMD) for April and May and omitting the 1983 data (as an outlier) we found that WUA and MMD were highly correlated with age-2 brown trout density (Table 4). In April 1983, while brown trout sac fry were immobile in the interstitial spaces in the gravel, flows were reduced 66% below the October 1982 spawning flows, probably resulting in failure of the 1983 year class. This was the justification for omitting the 1983 data pair.

On 25 May 1988, brown trout fry collected from the Arkansas River were larger

on average (33.3 mm TL), with the widest range in size (23–46 mm TL), than fry collected from any of the 11 study streams. Mean length of brown trout fry collected during June and July 1990–1992 was 45 mm TL, ranging in size from 35 to 61 mm TL, indicating that brown trout fry emergence occurs during April and May when high discharge and reduced habitat limit fry survival. Therefore, the significant correlations between age-2 density and June and July MMD are considered spurious.

Blue River. Age-2 brown trout density was correlated with MMD and fry WUA for May, June, and July 1984 (Table 4). Fry collections on the Blue River during the spring–summer months of 1988, and 1990 through 1992, revealed that brown trout fry emergence commenced in late May and continued into late July. On 23 May 1988, we collected newly emerged brown trout fry averaging 20.7 mm TL, ranging from 18 to 23 mm, indicating fry emergence had only begun. Additional collections during 1990, 1991, and 1992 revealed the presence of brown trout fry (≤ 26 mm TL) in June and July, but not in August, indicating that the correlations between brown trout density and fry WUA and MMD for May, June, and July 1980–1984 are valid.

Cache la Poudre River. Age-1 brown trout density was significantly correlated with brown trout fry WUA and MMD for June at five population study sites even though the most upstream sites were more than 50 km from the PHABSIM study area (Table 4). Rainbow trout density was correlated with July MMD and fry WUA at two sites. One site had restrictive angling regulations (artificial lures only, 406-mm minimum size limit) and the other site was closed to the public (Table 4). Fry sampling efforts from April through July 1988 revealed that brown and rainbow trout fry emergence occurred primarily during June and July, respectively.

Colorado River. The PHABSIM model revealed that four early life stages limited rainbow and brown trout populations (Table 4). At site 1, age-1 brown trout density was correlated with the differences in spawning flow (Δ MMD) and spawning habitat (Δ WUA) between October and March. Although it seems counterintuitive

TABLE 4
Significant ($P \leq 0.05$) correlations by time period between trout density at age (dependent variable) versus mean monthly discharge (MMD) and weighted usable area (WUA) (independent variables) for the critical life stages of brown and rainbow trout in 10 Colorado streams. Dashes (—) in the MMD and WUA columns indicate the correlation was nonsignificant. No significant relationships were found for the Fryingpan River.

Species	Age (year)	Life stage	Years data	Site no.	Time period	Correlation coefficients (r)	
						MMD	WUA
Arkansas River							
Brown	1	Fry	6	1	July	-0.85 ^a	—
Brown	2	Fry	6	1	June	-0.84 ^a	—
Brown	2	Fry	5	1	April-May	-0.90	0.92
Blue River							
Brown	2	Fry	5	1	May	-0.95	0.95
Brown	2	Fry	5	1	June	-0.84	0.91
Brown	2	Fry	5	1	July	-0.81	0.87
Cache la Poudre River							
Brown	1	Fry	7	1	June	-0.73	0.71
Brown	1	Fry	7	2	June	-0.79	0.71
Brown	1	Fry	7	3	June	-0.86	0.80
Brown	1	Fry	7	4	June	-0.84	0.82
Rainbow	1	Fry	7	5	June	-0.86	0.82
Rainbow	1	Fry	7	3	July	—	0.73
Rainbow	1	Fry	7	5	June	-0.82	0.82
Rainbow	1	Fry	7	5	July	-0.77	0.77
Colorado River							
Brown	1	Δ MMD, Δ WUA ^b	5	1	October-March	-0.94	-0.92
Brown	2	Spawning	6	2	November	-0.74	—
Brown	2	Hatching	6	2	April	-0.74	—
Brown	1	Fry	6	1	June	—	0.86
Brown	2	Fry	6	2	May	—	0.78
Rainbow	1	Fry	5	1	June 15-July 15	-0.90	0.98
Rainbow	2	Spawning	6	2	April 15-30	—	0.76
Gunnison River							
Brown	1	Fry	7	1	May	—	0.82
Brown	1	Fry	7	1	June	—	0.86
Brown	1	Fry	7	1	July	—	0.79 ^a
Brown	1	Fry	7	2	May	—	0.86
Rainbow	1	Fry	7	2	June	-0.71	0.81
Rainbow	1	Fry	7	1	May	—	0.73 ^a
Rainbow	1	Fry	7	1	June	-0.67	0.78
Rainbow	1	Fry	7	1	July	—	0.79
Rainbow	1	Fry	7	2	May	—	0.89 ^a
Rainbow	1	Fry	7	2	June	-0.73	0.92
Rainbow	1	Fry	7	2	July	—	0.74
Rio Grande River							
Brown	1	Fry	5	1	May	—	0.87
Brown	1	Fry	11	2	May	-0.68	0.74
Brown	1	Fry	11	2	June	-0.60	—
Brown	2	Fry	11	2	July	-0.78	0.71
Brown	2	Fry	6	3	May	-0.80	—
Brown	2	Fry	6	3	June	-0.96	0.83
Brown	2	Fry	6	3	July	-0.98	0.83

TABLE 4
Continued.

Species	Age (year)	Life stage	Years data	Site no.	Time period	Correlation coefficients (r)	
						MMD	WUA
South Fork of the Rio Grande River							
Brown	1	Fry	7	1	April	-0.74 ^a	—
Brown	1	Fry	7	1	July	-0.75	0.83
Brown	1	Fry	7	2	April	0.85 ^a	—
Brown	1	Fry	7	2	May	-0.84 ^a	0.75 ^a
Brown	1	Fry	7	2	June	-0.77	0.74
Brown	1	Fry	7	2	July	-0.88	0.89
Brown	1	Fry	7	3	April	-0.78 ^a	—
Brown	1	Fry	7	3	May	-0.74 ^a	0.68 ^a
Brown	1	Fry	7	3	June	-0.73	—
Brown	1	Fry	7	3	July	-0.91	0.87
St. Vrain River							
Brown	1	Fry	5	1	April	—	0.82
South Platte River							
Brown	0	Fry	9	1	May	-0.88	0.89
Brown	0	Fry	9	1	June	-0.84	0.89
Brown	0	Fry	9	1	July	-0.69 ^a	0.74 ^a
Brown	1	Fry	9	1	June	-0.90	0.84
Brown	1	Fry	9	1	July	-0.69 ^a	0.77 ^a
Rainbow	0	Fry	10	1	May	—	0.67 ^a
Rainbow	0	Fry	10	1	June	-0.77	0.84
Rainbow	0	Fry	10	1	July	-0.63	0.71
Rainbow	1	Fry	10	1	June	-0.75	0.75
Rainbow	1	Fry	10	1	July	-0.74	0.79
Taylor River							
Brown	1	Spawning	7	1	October	-0.70	—
Brown	2	Spawning	7	1	October	-0.89	—
Brown	1	Δ MMD, Δ WUA ^b	7	1	October-March	-0.71	—
Brown	2	Δ MMD, Δ WUA ^b	7	1	October-March	-0.92	-0.92
Brown	1	Incubation	7	2	January	0.83	0.84
Brown	2	Fry	7	2	June	-0.81	—
Brown	2	Fry	7	2	July	-0.76	—
Brown	2	Incubation	7	3	January	0.68	0.69
Brown	1	Δ MMD, Δ WUA ^b	8	3	October-March	—	-0.68
Brown	2	Fry	8	3	June	-0.78	—
Brown	2	Fry	8	3	July	-0.72	—

^a Field sampling failed to corroborate the presence of trout fry during the time period indicated by the correlation between habitat (MMD and/or WUA) and trout density; thus, the correlation is considered spurious.

^b Net change in discharge (MMD) and spawning habitat (WUA) between egg deposition and hatching due to discharge decreases during the winter months.

(see Discussion), November MMD and spawning WUA as well as April MMD (hatching flows) were negatively correlated with age-2 brown trout density at site 2 (Table 4). At site 2, age-2 rainbow trout density was correlated with rainbow spawning WUA (but not with spawning

flows) for the period of 15-30 April 1979-1984 (Table 4).

Rainbow and brown trout fry WUA limited trout populations in the Colorado River (Table 4). At site 1, age-1 rainbow trout density was correlated with fry WUA and MMD for the period 15 June-15 July 1982-

TABLE 5
Number of significant and nonsignificant correlations among 71 comparisons of trout density and weighted usable area (WUA) and between trout density and mean monthly discharge (MMD) for the 11 Physical Habitat Simulation (PHABSIM) study streams. Spurious correlations occurred when field sampling failed to yield trout fry ≤ 30 mm total length during a period of significant correlation between mean monthly discharge (MMD) or weighted usable area (WUA) and trout density.

Description of comparison	Density versus MMD		Density versus WUA
	Density versus MMD	Density versus WUA	
Significant correlations at $P \leq 0.05$	45/71	46/71	
Instances of nonsignificance where the parallel correlation was significant	12/71	11/71	
Instances of stronger correlation	21/71	29/71	
Instances of stronger correlation (fry only)	13/60	25/60	
Spurious correlations (for fry only)	9/60	8/60	

1986. Similarly, age-1 brown trout density and WUA were correlated for June 1981-1986 at site 1. Downstream at site 2, age-2 brown trout density was correlated with fry WUA for May 1979-1984. Fry collections during May-June 1988 verified differences in emergence times between the two sites. On 23 May 1988, brown trout fry collected at site 2 averaged 24.4 mm TL. No brown trout fry were observed at site 1 on that date. On 10 June 1988, brown trout fry were collected at both sites. On 22 June at site 1, newly emerged rainbow trout fry ranged from 22 to 26 mm TL (mean 23.3 mm TL) compared to an average of 40.5 mm TL for brown trout fry.

For the 1982 rainbow trout year class, density was approximately 2.2 times stronger than that of brown trout at site 1 even though fry WUA was better for brown trout than for rainbows. However, spawning WUA was 7.9 times greater for rainbow trout. Both 1983 and 1984 were extremely high water years and fry habitat was severely limited for both species, resulting in a decline in age-1 density. In 1985 and 1986, fry habitat conditions were good for both species, yet age-1 rainbow trout were more abundant than age-1 brown trout. Again, the rainbow trout spawning WUA was two- to three-fold greater during those years.

In contrast, age-1 brown trout density at site 1 was the highest in 1982, when brown trout spawning WUA was the lowest for the 8 years of study. However, the winter of 1981-1982 was the only year when mid-winter flows did not drop below the October spawning flows and June had the

highest level of brown trout fry WUA for the 8-year study. The result was the strongest age-1 brown trout year-class (1982) at site 1 during the 6 years of population evaluation.

From 1979 through 1986, population estimates at both study sites revealed that rainbow trout was the dominant species. A paired *t*-test comparison of the within-year rainbow and brown trout densities indicated that rainbow trout were significantly more abundant ($P \leq 0.01$) for an 8-year period. Similarly, a paired *t*-test analysis of within-year spawning WUA indicated rainbow trout had a significant ($P \leq 0.005$) advantage over brown trout in spawning habitat. A two- to four-fold advantage in spawning flows translated into a two- to eleven-fold advantage in spawning WUA. Within years, age-1 and -2 rainbow density was one to four times greater than that of brown trout.

Gunnison River. During a 7-year study, stream discharge was highly variable (Table 6), providing an opportunity to test rigorously the capability of the PHABSIM models to assess the biological impacts of extreme variations in physical habitat on a trout population. At site 1, age-1 rainbow and brown trout densities were correlated with fry WUA for May, June, and July 1980-1986 (Table 4). Similarly, rainbow trout fry WUA was correlated with age-1 rainbow trout density for May, June, and July 1980-1986 at site 2 (Table 4), and age-1 brown trout density was correlated with fry WUA for May and June. June MMD was significantly correlated with age-1 rainbow trout

TABLE 6
Annual and critical monthly discharge levels in the Gunnison River for the period of study (1980-1986) and in parentheses ranking (from 1 = highest to 21 = lowest) for 23 years (1964-1986) of record.

Year	Average annual discharge (m ³ /sec)	Mean monthly flow for critical months (m ³ /sec)			
		April	May	June	July
1980	40.0 (9)	45.9 (7)	60.2 (7)	52.5 (6)	29.7 (8)
1981	23.0 (14)	6.6 (21)	6.2 (21)	6.6 (21)	6.8 (18)
1982	22.3 (17)	12.8 (14)	11.9 (15)	21.5 (15)	21.6 (12)
1983	54.2 (4)	24.1 (11)	32.5 (10)	118.0 (3)	119.0 (3)
1984	83.2 (1)	65.1 (4)	127.0 (2)	227.0 (1)	128.0 (2)
1985	64.5 (2)	89.6 (1)	85.6 (4)	109.0 (5)	49.6 (6)
1986	53.6 (5)	41.3 (9)	67.6 (5)	35.8 (10)	85.5 (4)

density at both sites and with age-1 brown trout density at site 2 (Table 4).

In 1986 and 1987, sampling of brown trout fry on the Gunnison River indicated that emergence began the last week of April, peaked in May, and was completed by mid-June. Rainbow fry emergence began the first week in June, peaked the third week, and continued into July. The fry sampling efforts indicated that the correlations between May fry WUA and age-1 rainbow trout density at sites 1 and 2, and between July fry WUA and age-1 brown trout density at site 1 (Table 4) were spurious.

Rio Grande River. Age-1 brown trout density at site 1 was correlated with fry WUA but not with MMD for May 1981-1985 (Table 4). At site 2, age-1 brown trout density was correlated with fry WUA for May and July 1980-1990 and with MMD for May, June, and July. At site 3, age-2 brown trout density was correlated with fry WUA for June and July 1980-1986 and with MMD for May, June, and July. Brown trout fry collections over a 5-year period (1988-1992) verified these months as the critical period for brown trout fry emergence.

South Fork of the Rio Grande River. Age-1 brown trout density was correlated with July fry WUA for three study sites over a 7-year period (1976-1982) (Table 4). At site 2, density was correlated with May and June fry WUA. Age-1 brown trout density was correlated with MMD for April, May, June, and July 1976-1982 at two of three population study sites. Fry sampling from

May through August over a 5-year period (1988-1992) revealed that brown trout fry emergence began in mid-June and continued into July.

St. Vrain River. Age-1 brown trout density was correlated with fry WUA but not MMD for April 1979-1983 (Table 4). Brown trout fry collected on 25 May 1988 averaged 29.2 mm TL, ranging in size up to 34 mm TL, strongly indicating that emergence began in April.

South Platte River. Age-0 brown trout density was correlated with fry WUA and MMD for May, June, and July 1978-1986 on the South Platte River. Age-0 rainbow trout density was correlated with fry WUA and MMD for June and July 1978-1986, as was rainbow trout density and fry WUA for 1977 through 1986 (Table 4). Collections of brown trout fry averaged 24.4 mm TL on 12 May 1988, but few were present. On 25 May 1988, no rainbow trout fry were present but brown trout fry were abundant, averaging 26.2 mm TL. On 20 June 1988, both rainbow and brown trout fry were abundant; the former averaged 26.1 mm TL, and ranged in size from 22 to 33 mm TL, and the latter averaged 37.7 mm TL, and ranged from 34 to 46 mm TL. These data indicate that brown trout fry emerge in May and June and rainbow trout fry emerge in June and July in the South Platte River.

Taylor River. Two years of preflow stabilization and four or more years of postflow

TABLE 7
Number of brown trout ≥ 12 cm total length per kilometer in the Taylor River in October 1974 and 1975 (preflow stabilization) and October 1979–1982 (postflow stabilization).

Station	Average				
	1974 and 1975	1979	1980	1981	1982
1	1,629	2,975	2,823	2,728	4,656
2	1,572	2,460	2,531	2,013	2,228
3	1,917	3,641	3,741	2,784	2,904
4	1,654	2,825	3,665	4,031	3,211
Average	1,693	2,975	3,190	2,889	3,250

stabilization brown trout population estimates were available for investigating the trout density-habitat (WUA)-flow (MMD) relationships. With no significant difference between the prestabilization years, the 1974 and 1975 population data were averaged and compared to the postflow stabilization years (1979–1982). A one-way ANOVA (Student-Newman-Keuls test) revealed that all postflow stabilization years density estimates were significantly different from the prestabilization (1974 and 1975) estimates (Table 7).

Next, we used linear regression to determine if spawning, egg incubation, or fry habitat (and the associated stream dis-

DISCUSSION

After working intensively with PHABSIM models for more than a decade, we believe that this unique technology, when properly used and applied, has tremendous potential for determining minimum and optimum streamflow requirements for lotic ecosystems downstream from large scale impoundments. Although widely used for instream flow modeling (Reiser et al. 1989), relatively few studies attempted field validation of the methodology during the 1980's (Orth and Maughan 1982; Shirvell 1989). Our investigation and the work of Jowett (1992) in New Zealand are the two most extensive PHABSIM field validation studies known to us. Based on our results and those of Jowett (1992), we disagree with the suggestion of Mathur et al. (1986) "... that application of the Instream Flow Incremental Methodology (IFIM) in

charges) were correlated with brown trout population density (Table 4). At site 1, age-1 and -2 brown trout densities were correlated with the differences in spawning flow (Δ MMD) and spawning habitat (Δ WUA) between October and March. Although it seems counterintuitive (see Discussion), October MMD and spawning WUA were negatively correlated with age-2 brown trout density at site 1. At site 2, age-1 brown trout density was positively correlated with January incubation flows and age-2 density was negatively correlated with MMD for June and July over a 7-year period. Similarly, age-2 brown trout density was positively correlated with January incubation flows and negatively correlated with MMD for June and July at site 3 over an 8-year period. Age-1 brown trout density was negatively correlated with the difference in spawning habitat (Δ WUA) between October and March at site 3 (Table 4). At site 3, age-1 brown trout density was correlated ($r = 0.74$) with June fry WUA (but not June MMD) when regression analysis was performed on nontransformed data for the 8-year period. Natural log transformation of the data pairs reversed the significance of the correlations with June WUA and MMD. Sampling from May through August 1988–1992 indicated that brown trout fry emergence occurs during June and July on the Taylor River.

its present form should be abandoned." In our study and the New Zealand investigation (Jowett 1992), WUA and trout density were highly correlated in a positive manner, as Mathur et al. (1986) suggested is an essential result for a successful validation study.

Accounting for Intervening Variables

In three instances in our study, a data pair (WUA versus trout density) was discarded as a statistical outlier, which dramatically improved a correlation between habitat (WUA) and trout density. In all three instances, a logical biological explanation existed for considering the data points as statistical outliers.

First, on the Arkansas River, when the

1983 data pair was eliminated, the correlation coefficient between age-2 brown trout density and April–May fry WUA increased from 0.32 to 0.92. Minimum daily flows in April 1983 were 66% lower than the October 1982 spawning flows, the period of intragravel existence for Arkansas River brown trout alevins. We believe the near failure of the 1983 brown trout year class resulted from mortality of sac fry during the April 1983 low-flow period.

Second, on the South Platte River, we treated 1981 data as an outlier. Adequate intragravel flow of water is critically important to salmonid embryonic development (Reiser and White 1983; Neitzel and Becker 1985). In one study (Becker et al. 1982), a 1-hour daily dewatering of redds containing salmonid alevins resulted in 97% mortality of the sac fry. Another study (Becker et al. 1983) demonstrated that a one-time dewatering of salmonid redds for 6 hours resulted in 99% mortality of intragravel alevins. We suspect the same phenomenon led to the near failure of the 1981 year class of rainbow trout on the South Platte River. Here stream discharge dropped 91% between 23 May and 10 June 1981, compared to the April spawning flows. On 20 June 1988, rainbow fry samples were collected at the PHABSIM study site, indicating a late May to early June intragravel existence for rainbow trout sac fry. We believe the May 1981 flow reduction accounted for the differences in the density of age-1 rainbow trout between 1981 and 1982 (72/ha in 1981 versus 801/ha in 1982). Rainbow trout spawning flows and fry WUA in both years were near the maximum levels observed during the 10-year study. Again, this is adequate justification to consider the 1981 data pair as a statistical outlier.

Third, on the Colorado River, both rainbow trout spawning WUA and fry WUA were significantly correlated with rainbow trout density. Although spawning WUA in April 1983 was high, fry WUA was low, leading to low fry survival and low recruitment of juvenile rainbow trout to the 1983 year class. Elimination of the 1983 data point from the spawning regression analysis dramatically increased the correlation coefficient and level of significance.

Viewed simplistically, it seems counterintuitive that spawning (or incubation)

MMD and WUA for November as well as April MMD (hatching discharge) would be negatively correlated with age-2 brown trout density at site 2 on the Colorado River (Table 4). However, these data actually indicate that flow stability from egg deposition (in October–November) through hatching (April) is critical to brown trout year class recruitment. When the absolute differences in spawning flows (Δ MMD) and spawning habitat (Δ WUA) between October and March were regressed against age-1 brown trout density at site 1, the correlations were highly negative in both instances (Table 4), thus supporting the flow-stability hypothesis. We observed similar interactions between fall spawning flows and mid-winter flow reductions that affected brown trout recruitment on the Taylor River as well (Table 4).

Effectiveness of PHABSIM

Impoundments and massive transmountain diversions in the headwaters of the Colorado River result in severe seasonal distortion of the annual discharge hydrograph, eliciting unexpected responses in rainbow and brown trout population dynamics. Stream trout populations in Colorado managed with an eight trout per day bag limit and no terminal tackle restrictions are normally dominated by brown trout due to the much greater vulnerability of rainbow trout to angler harvest (Anderson and Nehring 1984). However, rainbow trout dominated the Colorado River trout population without the protection of minimum size angling regulations.

The PHABSIM model was an effective tool in elucidating this unusual relationship. Over an 8-year period (1979–1986), the model indicated that within-year differences in rainbow and brown trout fry WUA were small and each species had a slight advantage in fry WUA in 4 of 8 years. Thus, the value of fry WUA (for explaining rainbow trout dominance in the Colorado River) was equivocal. However, the model indicated rainbow trout spawning WUA was 2 to 11 times greater than that of brown trout for 6 of 8 years. Correspondingly, rainbow trout year class density was one to four times greater than that of brown trout.

Some users of PHABSIM models (Mathur et al. 1986) suggest that simple correlation of streamflow with population abundance or biomass might adequately describe the negative or positive impacts of flow variation on fish. Indeed, in our early work with PHABSIM on the South Fork of the Rio Grande River it appeared that this approach worked quite well. However, after studying 11 streams over a 10-year period, we conclude that this simplistic approach is not satisfactory. Although our results demonstrated that trout density was correlated with both WUA and MMD in 10 of the 11 streams we studied, the relationship between habitat (WUA) and trout density was more often highly correlated, which significantly improved our ability to explain variations in trout density. This was especially true for the fry life stage, which accounted for 67% of the significant correlations. The correlation between fry habitat (WUA) and density provided a stronger correlation coefficient twice as often as the fry MMD-density relationship (Tables 4 and 5). The density-fry WUA correlations more accurately and precisely defined the critical habitat "bottlenecks."

On 7 of 11 streams, we found that a single, well-placed representative PHABSIM study site provided significant correlations between habitat (WUA) and trout density for other population study sites many kilometers distant. Even in the face of considerable flow augmentation from tributary streams, habitat and trout density correlations remained strong as long as there were no dramatic differences in channel morphology between the PHABSIM and the population study sites.

The utility and adaptability of the PHABSIM model was well demonstrated. It proved useful in explaining the unusual relationship between the rainbow and brown trout populations of the Colorado River where rainbow trout dominance was largely the result of a significant advantage in the spawning arena. The PHABSIM model also indicated that a difference of 2-4 weeks existed in the emergence time of brown trout between sites 1 and 2 on the Colorado River, even though the sites were no more than a few kilometers apart. This difference was verified with collections of brown trout fry at both sites. On

streams where impoundment seriously modified the discharge hydrograph (i.e., the Colorado, South Platte, and Taylor rivers), the PHABSIM results demonstrated that there are often two habitat "bottlenecks" that must be circumvented for successful recruitment of a year class (see Table 4).

Simplifying Factors

In Colorado and much of western North America, snow melt predictably augments stream discharge during the spring, which is the period of rainbow and brown trout fry emergence. Large scale impoundment of stream ecosystems, an ongoing phenomenon for a century or more, controls stream discharge patterns. Temporal and spatial predictability of seasonal stream discharge facilitated the strong correlations of trout density with habitat (WUA) and discharge (MMD) in this study.

Other factors simplified our study as well. Our fish species assemblages were quite simple compared to those in the eastern United States. Random catastrophic flood events that often affect stream ecosystems and trout populations in other areas of the United States (Elwood and Waters 1969; Seegrist and Gard 1972; Hanson and Waters 1974) are uncommon in Colorado, where large impoundments ameliorate the effects of stochastic flood events.

Symposia and books have been devoted to the impact of impoundments on lotic ecosystems (Lillehammer and Saltveit 1984; Petts 1984). Conventional wisdom might suggest that observation of the biological responses of lotic species to ecosystem perturbation is all that is needed to understand how to rectify the situation. However, simplistic solutions are rarely adequate for explaining the nuances of complex interactions in aquatic ecology.

Much evidence documenting salmonid species interactions with habitat variables (Bachman 1984; Rimmer 1985), intraspecific and interspecific competition for food and living space (Fausch and White 1981; Bachman 1984), and the bioenergetics and strategies associated with the search and pursuit of forage (Fausch 1984; Puckett and Dill 1985) exists in the scientific literature. Ottaway and Clarke (1981) and Ottaway and Forest (1983) found that high water

velocity greatly impacted the ability of newly emergent brown trout alevins to maintain position in an artificial stream environment. Anderson and Nehring (1985) further elucidated the detrimental effects of high volume stream discharge and associated high water velocities, and fry habitat limitations on recruitment and survival of rainbow and brown trout in the South Platte River in Colorado. Shirvell (1990) found that chinook, coho, and steelhead salmonid fry preferred low-velocity (≤ 10 cm/sec) habitats downstream from instream rootwads.

Such investigations increase our understanding of the growth, survival, and success of a given species facing intraspecific or interspecific competition. However, controlled experiments, no matter how well they attempt to mimic the natural physical environment, invariably place constraints on some environmental variables (Butler and Hawthorne 1968; Baldes and Vincent 1969; Jenkins 1969; Kraft 1972; Fausch 1984; Rimmer 1985; Fausch and White 1986; Irvine 1986). The control placed on those variables (in order to clarify the response of the organism to a particular parameter) may mask or alter the response to the same experimental parameter in an uncontrolled environment. In our study, no manipulations of stream discharge or the fish populations were made to affect a response.

Orth (1987) identified important points that should be addressed to improve the use of instream flow-habitat models. We incorporated several of his suggestions in our research design. (1) Our studies of individual streams were of sufficient duration to allow fluctuations of more than three orders of magnitude in streamflow and WUA to be experienced by the trout populations. Thus, we believe potential impacts of environmental variation that could either mask relationships between WUA and trout density or create false correlations due to an inadequately short evaluation time were minimized. No experimental manipulations of flow were imposed to alter environmental conditions or affect trout population response. (2) Sport fish angling regulations and management strategies were, with the exception of the Frypan River, constant throughout the study. Nine of the 11 study

streams were under very restrictive angling regulations (either catch and release or a 406-mm minimum size limit) throughout the study. Thus, the potential for variations in sport fish management to alter trout population response to real habitat fluctuations was minimized. (3) The fish were large enough to be effectively collected by our electrofishing techniques, which gave reliable population estimates within stream study sites between sampling years. (4) Our fish species assemblages were simple compared to regions of the United States east of the Mississippi River. The target species in our study streams were either allopatric brown trout (six streams) or sympatric rainbow and brown trout populations, and no more than four to six nongame species. Thus, with two game species as target organisms, the analysis process using PHABSIM was relatively simple. (5) Because our study streams supported some of the best wild trout populations in Colorado, we could reasonably assume that invertebrate food supply, water temperature, water quality, and other potential limiting factors accounted for very little additional variability.

Although we assessed all life stages of rainbow and brown trout for significant correlations between WUA and fish density, it became apparent after 4-5 years of study that the early life stages (spawning, incubation, hatching, emergence, and early fry) were the most vulnerable to flow-induced variations in habitat. These life stages, due to a stationary nature or relative immobility, are unable to respond quickly (if at all) to flow-induced habitat variations. It is at these early life stages that the "bottleneck" habitat theory is most valid. The loss of a year-class (in the early stages of development) due to flow-induced changes in habitat carries through for the entire potential life span of that cohort. Not only is the cohort lost from a recreational standpoint, but all of the potential progeny from that cohort are lost as well.

For adult (≥ 200 mm) brown trout, Jowett (1992) found strong correlations between density and WUA in 59 sites on New Zealand trout streams. In contrast, we found no significant correlation between adult trout density and WUA. In the New Zealand study (Jowett 1992), but not in ours,

cover was a component in determining adult WUA. Other studies have documented the importance of cover for brown trout, the primary salmonid species in our study streams (Butler and Hawthorne 1968; Baldes and Vincent 1969; Bachman 1984). Omission of cover as a critical habitat factor for adult trout may have been a shortcoming in our study. Moreover, regressing average adult trout WUA for the summer period (April–October) against adult trout density may have been an inappropriate comparison.

Karr and Dudley (1981) identified at least six primary factors that influence the structural and functional characteristics of stream ecosystems, which govern the distribution and abundance of stream fishes. These factors include an energy source (food), water quality, temperature, physical habitat, flow regime, and biotic interactions. We agree with Orth (1987) that users of instream flow models must have a working knowledge of how these six factors interact in stream ecosystems in order to avoid unanticipated effects. Petts's (1984) hierarchical system describes the actions and interactions of these six factors (and others) as three orders of impact. His third order impacts (on fish and aquatic invertebrates) are reflections of first and second order impacts at lower trophic levels and within the physical environment. In actual regulated stream situations, all three levels of impact are constantly undergoing varying rates of change. Rarely is a state of dynamic equilibrium reached. The responsibility of aquatic resource managers is to determine flow regimes in regulated streams that, within a certain range, will adequately protect aquatic community assemblages.

For salmonid populations in mountainous regions, our results demonstrate that PHABSIM has the capability of identifying habitat-limiting events in riverine ecosystems. Properly applied, the PHABSIM

model has the potential to facilitate more holistic management of one of earth's most endangered resources—healthy free-flowing streams. Any technology, improperly applied, invariably leads to the error, bias, and confusion alluded to by Mathur et al. (1986). The PHABSIM model is not a universal cure-all; rather, it is one more assessment tool to be used judiciously. Mosley and Jowett (1985) concluded that estimation of WUA does not replace biological expertise, but can provide an objective basis on which biologists may apply professional judgment.

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