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Effect of Flow Fluctuations on Brown Trout in the Beaverhead River, Montana¹

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Abstract.—The effects of variable flows on standing crops of brown trout (*Salmo trutta*) in the Beaverhead River below Clark Canyon Reservoir, Montana, were studied from 1966 to 1980. Large flow fluctuations during or prior to peak spawning in mid to late October appear to have hindered reproduction, thus influencing the recruitment of age-I+ (yearling) brown trout. Flow decreases of 6.59–18.08 m³/s (54–74%) followed by or preceded by increases of 6.71–14.52 m³/s (80–369%) occurred during spawning periods that yielded five of the six poor yearling estimates (39–164 yearlings/1,967 m of stream). Fluctuations lasted 3–23 d, with each decrease and increase taking 2–3 and 1–6 d, respectively, to complete. The nine spawning periods that yielded estimates of 333–1,255 yearlings/1,967 m of stream were devoid of these fluctuations. The poor yearling crops, all of which were found in the years prior to 1974, in turn, limited the total standing crops of brown trout during much of the study. Relationships between yearling numbers and the magnitude of the spawning, incubation, rearing, and potential stranding flows were not evident. The disruption of spawning is the most likely means by which flow fluctuations could have hindered reproduction.

The effects of variable flow releases from Clark Canyon Reservoir, Montana, on the standing crops (numbers and biomass) of trout in the Beaverhead River were investigated by the Montana Department of Fish, Wildlife, and Parks in cooperation with the Bureau of Reclamation and East Bench Irrigation District from 1966–1980. The primary goal of this long-term study was to provide in-stream flow recommendations that would maintain a high quality fishery for wild trout in the upper river. The study, while not completely successful in meeting this goal, provided insight into the relationship between year-class strengths of brown trout (*Salmo trutta*) and flow characteristics during the spawning period. I discuss this relationship in this paper.

Study Area

The Beaverhead River lies in southwest Montana. It originates at the outlet of Clark Canyon Reservoir, a 1,980-hectare irrigation storage facility completed by the Bureau of Reclamation in 1964, and flows 128 km before joining the Big Hole River to form the Jefferson River. It drains

an area of about 12,950 km². Gradient is moderate, averaging 2.27 m/km.

Data presented in this paper were collected from a 1,967-m study section beginning 2.9 km below Clark Canyon Dam. Within the section, the channel width averages 25.3 m and the streambed consists primarily of cobble and gravel. Seventy-seven percent of the stream bank area supports a heavy growth of willows. Excellent overhead cover for trout is provided primarily by undercut banks and submerged or overhanging willows. Brown trout, rainbow trout (*Salmo gairdneri*), mountain whitefish (*Prosopium williamsoni*), burbot (*Lota lota*), white sucker (*Catostomus commersoni*), longnose sucker (*Catostomus catostomus*), mottled sculpin (*Cottus bairdi*), and longnose dace (*Rhinichthys cataractae*) inhabit the section.

The entire Beaverhead River has been managed for wild trout since 1964 when the last hatchery plant occurred. The study section was planted no later than 1957, although stocking likely ceased much earlier. Trout growth within the section is exceptional for the rivers of Montana, with age-II and -III brown trout averaging 0.38 and 0.74 kg, respectively, during the 14-year study. The upper 20.1 km of river, which includes the study section, presently supports one of the finest trophy trout fisheries in Montana (trophy trout are longer than 508 mm).

Flows in the study section are completely regulated by Clark Canyon Dam. Annually, flows are lowest during the nonirrigation season (approx-

¹ Portions of this study were presented at the Wild Trout III Symposium, Yellowstone National Park, September 24–25, 1984, in a paper titled "Some Trout-Flow Relationships in Montana." The symposium was sponsored by the Federation of Fly Fishers, Trout Unlimited, the U.S. Department of Interior, and the U.S. Department of Agriculture.

TABLE 1.—Fall estimates of numbers and biomass of age-I+ brown trout per 1,967 m of the Beaverhead River, 1966–1980.

Year	Number	Biomass (kg)
1966	55	22.2
1967	39	15.4
1968	474	232.4
1969	438	153.9
1970	164	65.8
1971	141	49.5
1972	158	49.0
1973	57	18.6
1974	908	292.4
1975 ^a		
1976 ^a		
1977	646	196.1
1978	333	110.5
1979	1,155	248.4
1980	1,255	386.7

^a No estimate.

mately October 16 to April 14) when water for the upcoming irrigation season (approximately April 15 to October 15) is stored in the reservoir and releases into the river are reduced. During the study, mean annual nonirrigation flows ranged from 3.15 to 13.22 m³/s and mean annual irrigation flows ranged from 8.55 to 24.63 m³/s. Average daily flows ranged from 1.61 to 38.63 m³/s.

Methods

Brown trout were sampled by means of a boat-mounted electrofishing unit. Captured fish were weighed and measured (total length), and scales were taken for age determinations. Some young-of-the-year and yearling fish were permanently marked by removing an adipose or pelvic fin and some fish over 203 mm long received numbered floy tags. Marked brown trout were used primarily to verify age determinations. Population estimates were made by Chapman's modification of the Petersen mark-recapture formula (Ricker 1975). A 9–15-d period was usually allowed between marking and recapture trips. As many as three marking and two recapture trips were made per estimate. Estimates of standing crops by age-groups and 95% confidence intervals were calculated by computerized methods summarized by Vincent (1971, 1974).

Standing crops of brown trout were estimated in the fall and spring from October 1966 to October 1980, except there were no fall estimates in 1975 and 1976 and no spring estimate in 1973. Fall estimates were made between September 20 and October 31, spring estimates between March 1 and April 3. Age-I+ (yearling) and age-II brown

trout were the youngest groups estimated in the fall and spring, respectively. Fall estimates of age-II+ and older brown trout generally were inflated due to the upstream movement of spawners into the study section, and these estimates were omitted. Fall estimates of age-I+ brown trout were assumed to be valid because this group is sexually immature and, therefore, not expected to engage in spawning movements.

Flows were measured at U.S. Geological Survey gage 06015400 located 2.3 km upstream from the head of the study section. The recorded average daily flows were increased by 0.99 m³/s from October to March and 1.27 m³/s from April to September to adjust for groundwater inflows between the gage and end of the study section.

Some relationships were tested by linear regression analyses (Snedecor and Cochran 1967). Relationships were considered significant at $P \leq 0.05$.

Results

Brown Trout Standing Crop Estimates

During the study, fall estimates of the number and biomass of yearling brown trout per 1,967 m of stream ranged from 39 to 1,255 and 15.4 to 386.7 kg, respectively (Table 1). The lower estimates were concentrated in the years prior to 1974, during which the estimated numbers and biomass of yearlings averaged 191 and 75.9 kg, respectively. From 1974 on, they averaged 859 and 246.8 kg, respectively.

In spring, the estimated number and biomass of age-II and older (total) brown trout per 1,967 m of stream ranged from 317 to 1,749 and 327.3 to 1,191.3 kg, respectively (Table 2). Total standing crops declined between 1967 and 1968, remained fairly stable from 1968 through 1974, began to increase in 1975, peaked in 1977, and remained at a high level through 1980.

Year-Class Relationships

Linear regression analyses were used to evaluate the influence of year-class strengths the previous year on the standing crops of the respective age-groups (II, III, and IV and older) of brown trout the following year (Figure 1). The size of a year class the previous year explained 85, 93, and 63%, respectively, of the annual variations in the numerical estimates of age-II, -III, and -IV and older fish. Year-class biomass the previous year explained 67, 93, and 46%, respectively, of the annual variation in biomass estimates. All relationships but one were significant at $P < 0.01$.

TABLE 2.—Spring estimates of numbers and biomass of brown trout per 1,967 m of the Beaverhead River, 1967–1980.

Year	Age-group II		Age-group III		Age-group IV and older		Total (±95% confidence interval)	
	Number	Biomass (kg)	Number	Biomass (kg)	Number	Biomass (kg)	Number	Biomass (kg)
1967 ^a	54	24.5					771±207	686.0±188.9
1968	65	29.5	133	96.7	173	201.1	371±106	327.3±90.3
1969	237	111.2	111	102.6	171	243.8	519±225	457.6±227.6
1970	151	64.5	205	176.2	144	194.8	500±113	435.5±111.7
1971	237	94.0	133	104.4	165	198.4	535±153	396.8±104.9
1972	74	31.8	121	100.3	209	291.9	404±81	424.0±99.9
1973 ^b								
1974	32	15.4	90	75.8	195	292.8	317±77	384.0±89.4
1975	467	184.3	61	54.9	142	228.4	670±125	467.6±101.2
1976	624	228.4	420	302.4	139	232.4	1,183±436	763.2±257.9
1977	864	303.7	410	302.8	475	584.8	1,749±396	1,191.3±385.4
1978	565	221.6	791	531.2	338	398.6	1,694±538	1,151.4±376.8
1979	329	134.2	535	390.2	442	479.7	1,306±445	1,004.1±372.0
1980	865	286.7	316	230.7	484	604.6	1,665±495	1,122.0±255.4

^a Only age-group II was separated from the total.

^b No estimate.

Based on the results of these and other analyses not presented here, I concluded that the annual variations in the total standing crops of brown trout primarily reflected the strengths of the yearling crops in past years. The relatively low total standing crops prior to 1975 were the result of a long series of relatively weak yearling crops, while a series of stronger yearling crops were responsible for the increases beginning in 1975 and for the high levels from 1977 through 1980. Thus, further evaluations focused on potential relationships between yearling numbers and stream flows.

Yearling Standing Crop and Flow Relationships

The standing crop of a given year class of brown trout was first estimated at age-I+ or approximately 2 years after the eggs producing that year class were deposited in the gravels. Each estimate of yearling brown trout could, therefore, reflect flow variations during the preceding 2 years, a time divided into spawning, incubation, and rearing periods. Flows during these three periods were examined to determine if they affected yearling survival.

Spawning period.—The pattern of flows during spawning (October 1 to November 30) showed a relationship with yearling numbers. To demonstrate this relationship, the average daily flows during the 1964–1978 spawning periods were plotted and arrayed according to the estimated number of yearlings produced (Figure 2). These plots were divided into three groups termed poor (39–164

yearlings per 1,967 m of stream), fair (333–646), and good (864–1,255). The 1973 and 1974 spawning periods were included in this analysis even though yearling estimates were not made in 1975 and 1976. For these 2 years, the estimated number of age-II brown trout the following spring was used as an index of yearling strength.

Spawning periods yielding five of the six poor yearling crops had large flow fluctuations during or prior to peak spawning in mid to late October. During the 1969, 1970, and 1971 spawning periods, average daily flows decreased and increased two times within 11–15 days. Flow decreases ranged from 6.57 m³/s (54%) in 1970 to 18.08 m³/s (74%) in 1971. Flow increases ranged from 6.88 m³/s (134%) in 1970 to 14.52 m³/s (369%) in 1971. Within 3 d during the 1965 spawning period, flows decreased by 14.63 m³/s (64%), then increased by 6.71 m³/s (80%). Within 23 d during the 1968 spawning period, flows increased by 7.75 m³/s (157%), decreased by 8.63 m³/s (66%), then increased by 7.44 m³/s (166%). Each decrease and increase during these five spawning periods took 2–3 and 1–6 d, respectively, to complete. There was a poor yearling crop in 1966 despite no large flow fluctuations during the 1964 spawning period; however, spawning followed the closing of Clark Canyon Dam in August. Unknown factors related to dam construction may have influenced reproduction in 1964.

Large flow fluctuations also occurred during spawning periods after which some fair and good yearling crops were produced (Figure 2). In 1 d in

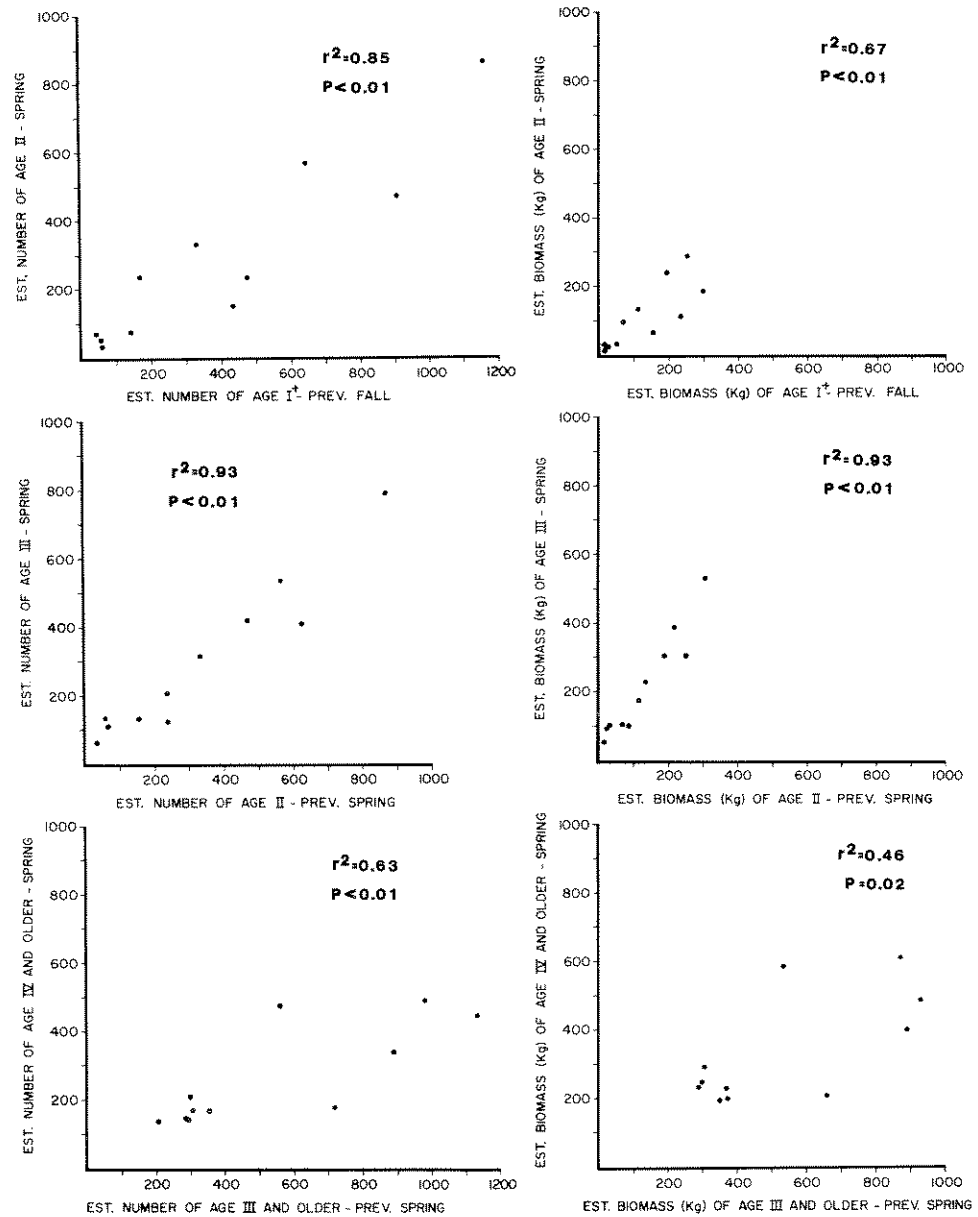


FIGURE 1.—Relationships between the estimated numbers and biomass of brown trout ages II, III, and IV and older and the year-class strength the previous year in the Beaverhead River, 1966–1980.

early October 1976, flow increased by 3.99 m³/s (41%), and during 4–8 d in October 1967, 1974, and 1975, flows decreased by 6.74 (65%), 10.16 (86%), and 8.15 m³/s (36%), respectively. These fluctuations were not followed by additional flow decreases or increases, as occurred during spawning periods that produced five of the six poor yearling crops.

To evaluate the relationship between the magnitude of “spawning” flows and yearling numbers, the minimum, maximum, and mean average daily flows during the 1964–1978 spawning periods were arrayed according to the estimated number of yearlings produced (Table 3). Minimum flows ranged from 1.61 to 13.33, maximum flows from 3.74 to 24.51, and mean flows from

3.27 to 17.09 m³/s. Yearling numbers were not related to minimum ($r = 0.06$; $P = 0.82$), maximum ($r = -0.38$; $P = 0.16$), or mean ($r = -0.40$; $P = 0.14$) flow. These data were retested after the nine estimates preceded by spawning periods having large flow changes as well as the 1966 estimate, which may reflect factors related to dam completion, were eliminated. Minimum, maximum, and mean spawning flows preceding the remaining five estimates (1968, 1974, 1975, 1979, and 1980) ranged from 2.32 to 10.61, 3.74 to 14.86, and 3.27 to 12.47 m³/s, respectively. Again, yearling numbers were not related to minimum ($r = 0.30$; $P = 0.62$), maximum ($r = 0.20$; $P = 0.75$), or mean ($r = 0.26$; $P = 0.67$) flow.

Incubation period.—The minimum, maximum, and mean average daily flows during the incubation period (December 1 to April 15) also were arrayed according to the estimated number of yearlings produced and were compared to the flows during the spawning period (Table 3). Two general categories were evident: (1) incubation periods having relatively stable flows similar in magnitude to those during spawning, and (2) incubation periods having some flows substantially less than the mean level during spawning. Those periods in which the minimum flow was 83–115% of the mean spawning flow were assigned to category 1. The incubation period preceding the 1976 yearling estimate also was assigned to category 1 because flows during much of the spawning period (October 15 to November 30) were relatively stable, ranging from 1.61 to 2.55 m³/s, and were similar to the “incubation” flows that ranged from 2.35 to 3.51 m³/s. The other incubation periods, having minimum flows equal to 22–49% of the mean spawning flows, were placed in category 2, which was assumed to have the greatest potential for egg and alevin losses resulting from dewatering of the redds. Category-2 incubation periods were associated with five of the six poor yearling crops, two of the five fair yearling crops, and one of the four good yearling crops. As yearling numbers increased, category-2 incubation periods were less numerous.

The evaluation was continued with the elimination of the nine estimates preceded by spawning periods having large flow changes plus the 1966 estimate. Fairly stable flows characterized the spawning periods preceding the yearling estimates in 1968, 1974, 1975, 1979, and 1980. Minimum incubation flows preceding these estimates were 87, 38, 83, 115, and 91%, respectively, of the mean flows during the spawning periods. Only the min-

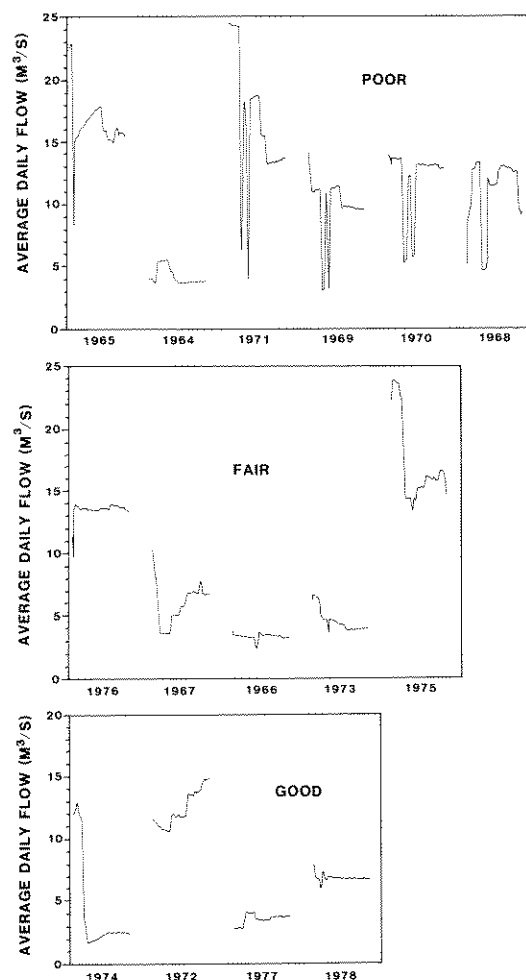


FIGURE 2.—Average daily flows (m³/s) in the Beaverhead River during the 1964–1978 brown trout spawning periods (October 1 to November 30) arrayed left to right from lowest to highest number of yearlings produced. Poor = 39–164 yearlings/1,967 m of stream, fair = 333–646, and good = 864–1,255.

imum incubation flow preceding the good estimate in 1974 was substantially less than the mean spawning level.

Rearing period.—The distributions of the number of daily flows within designated ranges during the approximate 17-month rearing period between the emergence of the brown trout fry (approximately April 16) and the fall yearling estimates were arrayed according to the estimated number of yearlings produced (Table 4). Based on the number of daily flows less than 2.84 m³/s, the three rearing periods having the lowest flows preceded the 1975, 1977, and 1978 estimates—all classified

TABLE 3.—Minimum, maximum, and mean average daily flows (m^3/s) in the Beaverhead River during the spawning and incubation periods preceding the fall estimates of age-I+ brown trout, 1966–1980. Brown trout estimates (number/1,967 m of river) are arrayed from lowest to highest.

Estimated number of brown trout (year of fall estimate)	Spawning period (Oct 1 to Nov 30)			Incubation period (Dec 1 to April 15)		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
39 (1967)	8.38	23.01	16.55	3.65	15.59	8.49
55 (1966)	3.62	5.46	4.16	3.54	4.70	3.79
57 (1973)	3.93	24.51	16.37	6.34	23.55	12.77
141 (1971)	2.97	14.12	9.73	3.76	10.27	7.83
158 (1972)	5.12	13.78	11.88	4.78	15.73	10.93
164 (1970)	4.47	13.22	10.69	5.24	23.91	10.67
333 (1978)	9.74	14.07	13.57	3.25	13.39	6.85
438 (1969)	3.54	10.33	5.94	5.58	10.61	8.01
474 (1968)	2.32	3.74	3.27	2.86	3.48	3.12
624 ^a (1975)	3.59	6.62	4.45	3.68	8.32	6.25
646 (1977)	13.33	23.91	17.09	5.83	17.09	12.01
864 ^a (1976)	1.61	12.96	4.04	2.35	3.51	2.88
908 (1974)	10.61	14.86	12.47	4.73	14.94	7.18
1,155 (1979)	2.77	4.13	3.55	4.08	5.74	4.98
1,255 (1980)	6.03	7.92	6.87	6.23	7.02	6.51

^a The estimated number of age-II brown trout the following spring was substituted because no yearling estimate was made.

as fair. Based on the number of flows less than $4.26 m^3/s$, the three rearing periods having the lowest flows preceded the 1967, 1975, and 1980 estimates, which were classified as poor, fair, and good, respectively. Rearing flows preceding the fair estimate in 1975 were the lowest of the study, with 13 daily flows less than $2.13 m^3/s$ and 112 flows less than $2.84 m^3/s$. The three rearing periods having the highest flows (based on no more than one flow less than $5.67 m^3/s$) preceded the 1972 estimate (classified as poor) and the 1976 and 1979 estimates (classified as good). A relationship be-

tween the magnitude of the flows during the rearing period and yearling numbers was not evident.

Relationships between "rearing" flows and yearling numbers were further evaluated by linear regression analyses. Flow statistics tested for each rearing period were (1) the lowest mean monthly flow, (2) the average of the three lowest mean monthly flows, and (3) the lowest mean monthly flow in winter (December–March), the season when trout are believed to be most stressed as a result of harsh physical conditions. Flows based on those three criteria ranged from 2.39 to 9.48, 2.47 to

TABLE 4.—Distribution of the number of daily flows (m^3/s) of designated ranges during the approximately 17-month rearing period preceding the fall estimates of age-I+ brown trout in the Beaverhead River, 1966–1980. Brown trout estimates (number/1,967 m of river) are arrayed from lowest to highest.

Estimated number of brown trout (year of fall estimate)	Daily flows (m^3/s)									
	1.61– 2.12	2.13– 2.83	2.84– 4.25	4.26– 5.66	5.67– 7.80	7.09– 8.50	8.51– 11.33	11.34– 14.16	14.17– 21.24	>21.25
39 (1967)	0	3	252	13	30	20	53	37	93	12
55 (1966)	0	0	21	12	68	79	32	49	224	22
57 (1973)	0	0	0	51	47	35	64	51	145	113
141 (1971)	0	0	0	8	5	7	77	108	78	234
158 (1972)	0	0	1	0	6	2	72	57	110	247
164 (1970)	0	0	5	9	19	114	103	45	93	135
333 (1978)	0	10	57	137	22	40	13	44	124	59
438 (1969)	0	1	2	8	3	60	129	69	147	100
474 (1968)	0	1	38	23	39	136	124	36	116	9
624 ^a (1975)	13	99	97	1	5	12	18	29	73	184
646 (1977)	0	6	41	50	23	38	37	123	75	117
864 ^a (1976)	0	0	0	0	5	10	89	79	120	216
908 (1974)	2	1	59	39	87	41	31	26	96	138
1,155 (1979)	0	0	0	0	235	34	18	24	65	117
1,255 (1980)	0	0	203	11	21	51	21	47	82	100

^a The estimated number of age-II brown trout the following spring was substituted because a yearling estimate was not made.

TABLE 5.—Lowest mean monthly flows, averages of the three lowest mean monthly flows, and lowest mean monthly flows in winter (December to March) during the rearing periods preceding the fall estimates of age-I+ brown trout in the Beaverhead River, 1966–1980. Brown trout estimates (number/1,967 m of river) are arrayed from lowest to highest.

Estimated number of brown trout (year of fall estimate)	Lowest mean monthly flow (m ³ /s)	Average of three lowest mean monthly flows (m ³ /s)	Lowest mean monthly flow in winter (m ³ /s)
39 (1967)	3.01	3.07	3.01
55 (1966)	4.09	5.54	6.08
57 (1973)	6.06	6.66	6.06
141 (1971)	9.06	10.07	9.06
158 (1972)	9.48	10.87	9.48
164 (1970)	6.74	7.03	6.74
333 (1978)	3.45	3.88	4.53
438 (1969)	7.95	8.38	7.95
474 (1968)	4.50	5.03	7.47
624 ^a (1975)	2.39	2.47	2.39
646 (1977)	3.77	4.47	3.77
864 ^a (1976)	7.75	8.88	9.40
908 (1974)	3.88	4.56	4.81
1,155 (1979)	6.25	6.37	6.25
1,255 (1980)	3.60	3.68	3.60

^a The estimated number of age-II brown trout the following spring was substituted because a yearling estimate was not made.

10.87, and 2.39 to 9.48 m³/s, respectively (Table 5). No relationships were found. These data were retested, eliminating the six poor yearling estimates, and again there were no relationships.

The number of times the average daily flows decreased by 30% or more within a 2-d period during the first 5½ months (April 16 to September 30) of the approximate 17-month rearing period were compiled and arrayed according to the estimated number of yearlings produced (Table 6). Decreases of this magnitude during this period were assumed to have the potential to strand young brown trout. One to three flow decreases of 30% or more preceded four of the six poor yearling crops, three of the five fair yearling crops, and two of the four good yearling crops. A relationship between potential stranding flows and yearling numbers was not evident.

Discussion

Of the flow characteristics evaluated during the spawning, incubation, and rearing periods, the pattern of the spawning flows in the Beaverhead River showed the strongest relationship with numbers of yearling brown trout produced during the 14-year study. Spawning flow decreases of 6.57–

TABLE 6.—Number of times the average daily flows decreased by 30% or more within 2 d during the first 5½ months (April 16 to September 30) of the approximately 17-month rearing period preceding the fall estimates of age-I+ brown trout per 1,967 m of the Beaverhead River, 1966–1980. Brown trout estimates are arrayed from lowest to highest.

Estimated number of brown trout (year of fall estimate)	Number of decreases (% decrease)
39 (1967)	0
55 (1966)	3 (33, 49, 70)
57 (1973)	2 (31, 32)
141 (1971)	1 (42)
158 (1972)	0
164 (1970)	1 (30)
333 (1978)	1 (42)
438 (1969)	1 (73)
474 (1968)	2 (44, 47)
624 ^a (1975)	0
646 (1977)	0
864 ^a (1976)	3 (38, 48, 58)
908 (1974)	2 (36, 50)
1,155 (1979)	0
1,255 (1980)	0

^a The estimated number of age-II brown trout the following spring was substituted because a yearling estimate was not made.

18.08 m³/s (54–74%) followed or preceded by increases of 6.71–14.52 m³/s (80–369%) appear to have hindered reproduction, thus contributing to the series of poor yearling crops prior to 1974. These poor yearling crops, in turn, limited the total standing crops of brown trout during much of the study. These flow fluctuations primarily resulted from the Montana Department of Fish, Wildlife, and Parks requesting lower flow releases at Clark Canyon Dam to facilitate the completion of the fall mark–recapture estimates. Once this practice was discontinued, yearling stocks improved dramatically.

A possible relationship between yearling numbers and flow reductions during the incubation period also was noted. However, the significance of this finding is mitigated by the fact that a substantial flow reduction occurred during the incubation period preceding the good yearling crop in 1974 (Table 3). The minimum incubation flow preceding this estimate was 38% of the mean spawning flow and 45% of the minimum spawning flow. Furthermore, lower flows occurred towards the end of this incubation period (March 9 to April 15) when alevins, reported to be more sensitive to dewatering than the egg phases (Becker et al. 1983), were expected to be in the gravels. During this 38-d period, minimum, maximum, and mean incubation flows were 4.73, 5.91, and 5.42 m³/s,

respectively, or 45, 40, and 43%, respectively, of the minimum, maximum, and mean spawning flows. It is unlikely that a good yearling crop would have followed had flow reductions during incubation been an important limiting factor.

The means by which flow fluctuations could have hindered brown trout reproduction were not investigated during the study. The dewatering of completed redds provides an unlikely explanation due to the reported tolerance of salmonid eggs to extended periods of dewatering. In laboratory studies using artificial redds, Becker et al. (1983) found 92–98% survival of chinook salmon (*Oncorhynchus tshawytscha*) cleavage eggs and embryos after 12 consecutive days of dewatering. Hatching success of steelhead (*Salmo gairdneri*) and chinook salmon eggs placed in experimental channels was unaffected by 1–4 and 1–5 weeks of continuous dewatering, respectively (Reiser and White 1983). Hobbs (1937) found 83% viable eggs in natural brown trout redds that had been dewatered for about 5 weeks. The maximum period that some redds in the Beaverhead River could have been continuously dewatered during those spawning periods that resulted in poor yearling estimates was 9 d—well within the tolerances reported by the above authors. The failure of the large flow reduction during the incubation period preceding the 1974 yearling estimate to depress yearling numbers further supports the contention that the dewatering of redds was not an important limiting factor.

Brown trout in the Beaverhead River select a fairly limited range of depths and current velocities when spawning. Ninety percent of the 77 redds measured by Sando (1981) were found at depths of 18–46 cm, where water velocities were 0.35–0.95 m/s. Consequently, it is conceivable that the wide-ranging and rapidly changing depths and velocities associated with large flow fluctuations interfered with the selection of spawning sites and the successful completion of the spawning act, thus hindering reproduction and the recruitment of young.

The disruption of spawning by flow changes has been observed in other studies. Abrupt flow increases ($\geq 50\%$) or decreases ($\geq 30\%$) below a power plant on the Campbell River in British Columbia caused chinook salmon to repeatedly start redds and abandon them before completion, with the level of disruption related to the magnitude of the flow changes (Hamilton and Buell 1976). Substantial losses of viable eggs occurred due to the untimely release of eggs, the failure to cover eggs

once released, and the failure to properly fertilize eggs. Disrupted fish, particularly during decreasing flows, ultimately abandoned the spawning areas and seldom returned after flows were stabilized at their original levels. Bauersfeld (1978) observed that daily flow fluctuations below a Columbia River dam resulted in the construction of atypical redds by chinook salmon, even in those areas that were wetted throughout the spawning period. Redds lacked a large tailspill believed by Bauersfeld to protect eggs from scouring and predators and were larger than normal, suggesting fish were having difficulty in locating preferred spawning areas. Approximately 54% of the redds in the zone of fluctuation contained no eggs and those with eggs may have contained less than the full complement, indicating that flow fluctuations caused fish to construct more than one redd (also reported by Hamilton and Buell 1976). Neither study evaluated annual recruitment levels before and after fluctuations occurred so that the impact of the observed spawning alterations on the numbers of young was undetermined.

Other studies evaluating flow fluctuations reported less disruptive impacts on spawning salmonids. Chapman et al. (1982) were unable, in a follow-up study, to confirm most of the previously discussed findings of Bauersfeld (1978). Redds were found to be normal in size and have tailspills, although tailspills were considered to provide no protection to embryos. Live embryos were found in 84% of the redds in the zone of fluctuation; however, whether or not they contained the full egg complement was undetermined. Chinook salmon forced off redds by daily flow fluctuations returned to complete their redds at increased flows. This was reported also by Stober et al. (1982) for salmon in the Skagit River, Washington. In spite of these findings, the disruption of spawning remains the most likely means by which flow fluctuations could have hindered brown trout reproduction in the Beaverhead River.

During this study, stream flow was considered the overriding factor controlling the standing crops of yearling brown trout, a reasonable assumption because the flow was completely regulated and subject to wide seasonal and annual variations. However, other factors also have periodically played a role. For example, a September 1967 fish kill attributed to hydrogen sulfide in reservoir releases was reported to extend into the study section (Wiperman and Elser 1968). This kill likely contributed to the low number of yearlings in fall 1967 as well as the total standing crop reduction be-

tween the spring of 1967 and the spring of 1968 (Tables 1, 2). Other factors could have influenced yearling recruitment as well, thus explaining the poor relationships between flow levels and yearling numbers obtained in the study. The poor relationship also could be the result of the simple analytical approach necessitated by the limited data. If stream flow is the overriding limiting factor, yearling numbers would likely reflect a combination or series of flow events during the 2 years between spawning and the yearling estimate—a period involving all brown trout life stages, each with separate flow needs. Unraveling the complex flow interactions that could have influenced yearling recruitment requires far more data than were collected in this study.

This study, while unable to conclusively prove that flow fluctuations during spawning were the primary cause of the poor yearling crops in the Beaverhead River, should alert managers to the importance of thoroughly evaluating fluctuations when assessing the potential impacts of altered flows on reproducing salmonid populations, particularly in areas slated for power-peaking projects. Power-peaking evaluations should include an assessment of recruitment levels following test spills during spawning and a comparison of these levels to the norm for the affected waters. The Beaverhead River study results suggested that the reproductive potential of brown trout would be severely limited by such flow regimes. Considerably more research is needed before the impacts of flow fluctuations on salmonid reproduction are fully understood.

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