

How High Can Brook Trout Jump? A Laboratory Evaluation of Brook Trout Jumping Performance

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Abstract.—Quantitative data on how high brook trout *Salvelinus fontinalis* can jump are crucial for efforts by fisheries managers to exclude brook trout from streams containing native cutthroat trout *Oncorhynchus clarkii* subsp. and to build effective fishways for brook trout migration. We identified factors that could influence brook trout jumping ability and demonstrated how this knowledge could be applied to improve the design of barriers to brook trout migration or fishways to facilitate their migration. Our objective was to measure brook trout jumping performance under laboratory conditions to identify design features for constructing waterfall-type barriers or pool-and-weir-type fishways. We used flashboard-type and flume-type adjustable waterfall devices to measure brook trout jumping performance at various combinations of vertical or waterfall height (13.5–93.5 cm in 10-cm increments) and plunge pool depth (10–60 cm in 10-cm increments) over a 24-h interval. We tested three size-classes of brook trout: 10–15 cm total length (TL) (mean \pm SD: 13.09 \pm 1.67 cm), 15–20 cm (19.30 \pm 1.19 cm), and 20 cm or more (26.52 \pm 2.13 cm). The 10–15-cm brook trout could jump a 63.5-cm-high waterfall, equivalent to 4.7 times their body length, from a 50-cm-deep plunge pool, which was 3.7 times their body length. Larger size-classes were capable of jumping 73.5-cm waterfalls, or 2.9–4.0 times their body length, provided the plunge pools were at least 40 cm deep (>1.6 times their body lengths). Shallow plunge pools (10 cm) prevented brook trout from all size-classes from jumping waterfalls 43.5 cm or more in height. Small fish were capable of jumping a greater number of body lengths over vertical obstacles than large fish. The data analyses identified vertical height, plunge pool depth, fish total length, and fish condition as factors important in predicting brook trout jumping performance.

Over the past two centuries, human activities have significantly changed the form and function of lotic systems throughout North America. In some cases, humans have eliminated physical and geographic barriers that once kept many fish species separate. This has led to an increased number of ecological interactions between native and introduced fishes (Dill and Cordone 1997; Richter et al. 1997). The outcomes of these interactions vary, but in many cases, introduced fishes out-compete native fishes for food and habitat resources, leading to declines or local extinctions of the native species (Griffith 1988). Miller et al. (1989) identified habitat alterations (in 73% of all recorded extinctions) and the effects of nonnative species (in 68% of all recorded extinctions) as the top causal factors behind extinctions of North American fishes during the 20th century. In the western United States, for example, introductions of nonnative salmonids threaten native cutthroat trout *Oncorhynchus clarkii* subsp. The development or modification of lotic resources has also led to the installation of structures, such as dams, that serve as obstacles or

barriers to bidirectional fish movements. This loss of ecological connectivity has affected a number of fish species, thereby isolating populations (Schlosser and Angermeier 1995) and in extreme cases causing local extinctions (Winston et al. 1991) as downstream populations were not able to recolonize upstream areas.

Brook trout *Salvelinus fontinalis* is a species that has benefited from the elimination of natural and human-made barriers, yet they have also experienced the detrimental effects of new instream barriers. In the Rocky Mountain region, brook trout were widely introduced to supplement populations of cutthroat trout subspecies that had declined from habitat alteration and overexploitation during the 1800s (Wiltzius 1985; Meehan and Bjornn 1991). Many of these introductions were successful, and self-sustaining populations of brook trout now occur in streams that once contained only cutthroat trout (MacCrimmon and Campbell 1969). In areas where sympatric populations are found, brook trout typically outcompete cutthroat trout for food and habitat resources (Griffith 1972; Fausch 1989; De Staso and Rahel 1994). Multiple studies have produced strong evidence implicating brook trout in the decline, and in some cases extinction, of native cutthroat trout populations (Griffith 1988; Behnke 1992). Cutthroat trout populations in areas free

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of brook trout are confined to headwater reaches that are protected by natural barriers to upstream brook trout movement (Harig et al. 2000; Novinger and Rahel 2003). Resource managers have been working to restore or reintroduce additional cutthroat trout populations using a variety of strategies (Stuber et al. 1988; Young et al. 1996). The most successful strategy consists of chemically treating sections of streams to eliminate all fishes, followed by the reintroduction of cutthroat trout (along with the original native fish assemblage) above a natural or artificial barrier, most often a waterfall or other similar drop-structure, that prevents upstream migration of any fish species (Behnke and Zarn 1976; Thompson and Rahel 1998). Information on the features of a drop-structure that effectively prevents brook trout from moving upstream is needed to facilitate the evaluation of the barrier potential of existing natural obstacles and the design and construction of artificial barriers.

Within their native range, brook trout, like many other stream fishes, have been affected by artificial instream structures such as dams (Winston et al. 1991), culverts (Dimeo 1977), and road crossings (Baxter et al. 1999). If these structures restrict or altogether prevent the upstream movement of fish, they can fragment fish populations, increasing the likelihood of local extirpations. The habitat of brook trout within their native range has been altered in this fashion, and in an ironic parallel to the situation in the Rocky Mountain region, Appalachian brook trout populations are facing competitive pressures from introduced salmonids, particularly rainbow trout *O. mykiss* and brown trout *Salmo trutta* (Moore et al. 1983; Larson and Moore 1985). Thus, information about brook trout jumping ability would allow managers to evaluate existing instream structures such as culverts and low-head dams to determine whether they serve as impassable barriers. Additionally, data on brook trout jumping performance could be used to optimize the designs of pool-and-weir type fishways (Clay 1995) to mitigate the effects of some of these structures.

Brook trout negotiate vertically oriented instream obstacles by jumping over them. The ability of brook trout to jump over obstacles depends on a number of physical and biological variables that have been the subject of surprisingly few quantitative studies. Stuart (1962) found that waterfall height, plunge pool depth, fish size, flow, light level, and characteristics of the standing wave all affected the jumping ability of Atlantic salmon *S. salar*, brown trout and Eurasian minnow *Phoxinus phoxinus*. More recently, Reiser and Peacock (1985) developed the following formula for computing the maximum height attainable by a fish:

$$h_1 = v^2/2g,$$

where h_1 is the leap height of the fish, v is the initial burst speed of the fish, and g is gravitational acceleration. This formula assumes the optimal jumping conditions proposed by Stuart (1962) of a minimum pool depth of 2.5 m or 1.25 times the waterfall height.

Aaserude and Orsborn (1985) developed a more refined expression using maximum burst velocity, velocity exiting the pool, fish weight, fish length, fish frontal area, and estimated drag forces to calculate maximum jumping heights for chum salmon *O. keta*, pink salmon *O. gorbuscha*, sockeye salmon *O. nerka*, coho salmon *O. kisutch*, and Chinook salmon *O. tshawytscha* as well as steelhead (anadromous rainbow trout) and coastal cutthroat trout (*O. clarkii clarkii*). In this expression, jumping heights could be calculated both from still pools and by fish using a standing wave generating a 0.5-m/s vertical flow velocity. Powers and Orsborn (1985) used these maximum jump height calculations for the same salmonids to construct theoretical jumping curves (for determining maximum jump height and jump distance) that vary with the angle at which a fish takes off from the water surface. To date, however, no studies directly measuring brook trout jumping performance have been published.

Our objective was to determine how high brook trout could jump when challenged with a range of waterfall heights and plunge pool depths. Our primary goal was to determine how waterfall height (H_1), plunge pool depth (H_2), and fish size influenced brook trout jumping performance. Our secondary goal was to develop a predictive model of brook trout jumping performance. Our a priori predictions for brook trout jumping performance were as follows: (1) brook trout jumping ability would be limited by some combination of shallow plunge pool depths and high waterfall heights, (2) a maximum waterfall jumping height exists for brook trout jumping under optimal conditions, and (3) large fish would jump higher than small fish under identical conditions, in much the same way that large fish have higher absolute swimming velocities than small fish (Bainbridge 1958; Fry and Cox 1970).

Methods

Brook trout jumping experiments were conducted at the Colorado Division of Wildlife Fish Research Hatchery in Bellvue. Experiments were conducted from July 2002 through April 2003 under a natural photoperiod (40°37'31" N) using air-equilibrated well water at $11 \pm 1^\circ\text{C}$. The well water chemistry was as follows: pH, 7.5; alkalinity, 185 mg/L as CaCO_3 ; hardness, 248 mg/L as CaCO_3 ; Cl^- , 5.02 mg/L; total dissolved solids, 418 mg/L; and $\text{NO}_3\text{-N}$, 5.03 mg/L.

TABLE 1.—Scoring system used to assess fin condition of fish. Overall fish condition was determined as the sum of this score and those for the jaw, eyes, and opercula (see Table 2).

Body part	Level of damage			
	None (>95% intact)	Mild (80–95% intact)	Moderate (50–80% intact)	Severe (<50% intact)
Fin				
Pectoral ^a	3	2	1	0
Dorsal	3	2	1	0
Pelvic ^a	3	2	1	0
Anal	3	2	1	0
Caudal	3	2	1	0

^aLeft or right.

Brook trout eggs from the Ten Sleep Hatchery in Wyoming were incubated at 11.7°C until 99% had hatched; sac-fry were then transferred to indoor rearing troughs. Fry were fed a 50:50 diet of Fry Feed (Kyowa size B-400, Kyowa Hakka Kogyo) and soft moist Silver Cup #0-starter. At 10 cm total length (TL), fry were transferred to outdoor raceways and fed ad libitum rations of Silver Cup commercial trout feed. Experiments were conducted on brook trout of 10 cm or more.

Brook trout jumping performance was measured in flashboard- and flume-type adjustable waterfall devices (Kondratieff and Myrick 2005). We used an incomplete three-way factorial design to examine the effects of waterfall height (13.5–93.5 cm in 10-cm increments), plunge pool depth (10–60 cm in 10-cm increments), and fish size (10–15, 15–20, and ≥20 cm TL). We only tested 110 of a possible 162 treatment combinations because we ceased conducting jumping trials for a given fish size-class and pool depth when two successive waterfall heights had been tested without any successful jumps. We used a similar protocol with plunge pool depths, except that we tested at least one depth below the level that prevented fish from successfully jumping a waterfall of fixed height. Each treatment combination had four replicates, resulting in 440 24-h jumping trials using 11,005 brook trout.

At the start of each jumping trial, waterfall height and plunge pool depth were set and the flow was adjusted to 570 L/min. A random sample of 25 brook trout from a precrowded raceway was then placed into the plunge pool and the translucent raceway cover closed. Fish were given approximately 24 h to move upstream past the waterfall (mean trial duration, 22.8; SD, 1.4 h). Fish were removed from the apparatus at the end of the trial and kept segregated by location (upstream versus downstream). Any fish found upstream of the waterfall at the end of the trial was classified as “successful” and all other fish were classified as “unsuccessful.” The number of jump

attempts required for a given fish to become “successful” is uncertain, since we did not track individual fish. The proportion of brook trout successfully jumping over the falls was calculated as the number of fish captured upstream of the waterfall divided by the total number fish (25) originally placed downstream. Brook trout were then lightly sedated (25 mg/L tricaine methanesulfonate buffered with 0.1 g/L NaHCO₃) and had their total lengths (cm) and wet weights (nearest 0.1 g) measured. Each fish received a physical condition score based on fin, eye, operculum, and jaw conditions (Tables 1, 2). Fish were categorized as “bad” if the summed scores were ≤3 and “good” if the summed scores were >3. The gender of sexually mature fish (≥20 cm) was noted; fish in the two smaller size-classes were not sexed. Processed fish were moved to a separate raceway.

Data from trials using the flashboard-type and flume-type waterfalls were analyzed together because pilot trials (Kondratieff and Myrick 2005) using Rio Grande cutthroat trout *O. c. virginalis* showed that the two types produced similar results. The probability (P) of a brook trout successfully jumping the waterfall was assumed to be a function of waterfall height (H_1), pool depth (H_2), total length (TL), condition (C), and trial duration (D) as well as the second-order interactions between the variables. We generated a series of multiple logistic regression models based on the global model shown below. A random component was used to check for evidence of extrabinomial variation (EBV) and to adjust confidence intervals for the beta estimates.

The global model was as follows:

$$\begin{aligned} \text{Logit}(P) = & \beta_0 + \beta_1(H_1) + \beta_2(H_2) + \beta_3(\text{TL}) + \beta_4(C) \\ & + \beta_5(D) + \beta_6(H_1 \times H_2) + \beta_7(H_1 \times \text{TL}) \\ & + \beta_8(H_1 \times C) + \beta_9(H_1 \times D) \\ & + \beta_{10}(H_2 \times \text{TL}) + \beta_{11}(H_2 \times C) \\ & + \beta_{12}(H_2 \times D) + \beta_{13}(\text{TL} \times C) \\ & + \beta_{14}(\text{TL} \times D) + \beta_{15}(C \times D) + \text{EBV}. \end{aligned}$$

A mixed-modeling approach (proc NLMIXED; SAS

TABLE 2.—Scoring system used to assess the condition of the jaw, eyes, and opercula. Overall fish condition was determined as the sum of these scores and that for fins (see Table 1).

Body part	Level of damage	
	Normal or no damage	Damage
Jaw	Normal = 1	Over- or underslung = 0
Eye ^a	No damage = 1	Damage = 0
Operculum ^a	Normal = 1	Eroded = 0

2003) and Akaike’s information criterion (AIC_c ; second-order variant for $n/K < 40$) model selection were used to identify the model that best determined P . We ranked the relative importance of each predictor variable occurring within the candidate model set by summing the AIC_c weights across all models within the set; the most important variables had the largest predictor weights and the least important ones the smallest predictor weights (Burnham and Anderson 2001).

Results

Brook trout jumping success was most affected by waterfall height, plunge pool depth, and fish size (Figure 1). Ten- to 15-cm fish jumped over waterfalls as high as 63.5 cm (4.7 body lengths) when plunge pools were 50 cm deep (3.7 body lengths) but did not jump over waterfalls 33.5 cm high or more when plunge pool depths were 10 cm. Fifteen- to 20-cm fish jumped over waterfalls as high as 73.5 cm (3.7–4.0 body lengths) when plunge pools were 40 or 50 cm deep but did not jump over waterfalls 33.5 cm high or more if the plunge pool depths were 10 cm. Fish 20 cm or more in size could jump over waterfalls as high as 73.5 cm (2.9 body lengths) when plunge pools were 40 cm deep but were limited by waterfalls 43.5 cm high or more when plunge pools were 10 cm deep.

Of the derived models, three had AIC_c values within 3 units of the smallest AIC_c value, which indicates the best model. The best model, model 1, was as follows (Table 3):

$$\begin{aligned} \text{Logit}(P) = & 4.81 - 0.17(H_2) - 0.03(H_2) + 0.089(TL) \\ & - 0.48(C) - 0.0017(D) \\ & + 0.0017(H_1 \times H_2) - 0.0016(H_2 \times TL) \\ & - 1.12(EBV). \end{aligned}$$

The four top models all included waterfall height, plunge pool depth, fish size, fish condition, a waterfall height \times pool depth interaction term, and a term for extrabinomial variation (Table 3). Model 1 also included trial duration and the pool depth \times total length interaction term (Table 4). There was strong evidence of waterfall height, total length, fish condition, and $H_1 \times H_2$ effects because the 95% confidence

intervals for the β estimates of these predictor variables did not include zero; there was also strong evidence of extrabinomial variation (Table 4). There was weaker evidence of trial duration, pool depth, and $H_2 \times TL$ effects. The most important predictor variables included waterfall height, pool depth, total length, fish condition, duration, and the interaction $H_1 \times H_2$ (Table 5; predictor weights ≥ 0.91). No other second-order effects were as important (Table 5). The best model showed that P decreased with increasing height, pool depth, and experimental duration and that P increased with increasing total length and fish condition. Fish that were in good condition (intact fins) were predicted to jump higher than those with heavily damaged fins. The analyses using sexually mature fish (≥ 20 cm) detected no evidence of a difference between male and female fish jumping ability ($N = 3,351$; males = 1,314; females = 2,037).

Discussion

We used adjustable waterfall devices to conduct the first comprehensive study on how waterfall height, pool depth, and fish size affect brook trout jumping performance under laboratory conditions. We found that the highest obstacle that 8.6–34.0-cm brook trout would jump over was 73.5 cm high, provided the pool below was at least 40 cm deep. This may not be the absolute maximum height that brook trout can jump, but it does represent a conservative estimate of their maximal performance. Shallow plunge pools severely reduced jumping ability, brook trout only being able to jump a maximum of 33.5 cm from a 10-cm pool. Brook trout 15 cm or longer could jump greater absolute heights than fish under 15 cm under identical experimental conditions. However, the small brook trout had higher relative jumping performance than the large fish, a relationship similar to that seen for salmonid swimming performance (Bainbridge 1958; Fry and Cox 1970). Small fish (10–15 cm) were capable of jumping up to 4.7 times their body length; 15–20-cm-long fish were capable of jumping up to 3.7–4.0 times their body length; and fish 20 cm or longer were capable of jumping 2.9 times their body length.

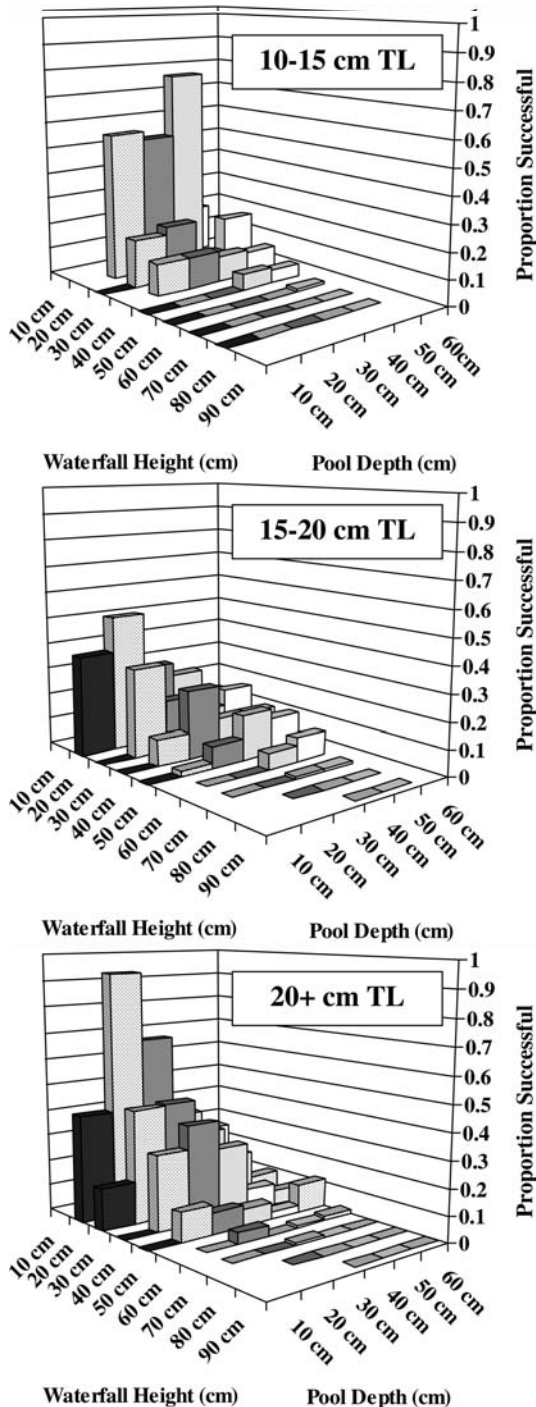


FIGURE 1.—Total proportion of brook trout (out of four combined replicate batches of 25 fish) jumping over a waterfall of fixed height and fixed pool depth for three fish size-classes. The Z-axis shows the proportion of fish successfully jumping over the falls, the X-axis shows pool depth, and the Y-axis shows waterfall height. Blank spaces on the X–Y plane represent height \times depth combinations for which no data were collected.

Our results support Stuart's (1962) field and laboratory observations that waterfall height, pool depth, and fish size all influence fish jumping performance. We also determined that the fish's physical condition, particularly fin condition, affects their jumping ability. There was also evidence of complex interactions between waterfall height and pool depth and between total length and pool depth. Evidence of extrabinomial variation suggests that other factors that were unaccounted for may influence fish jumping performance and warrant further investigation. One cause of this extrabinomial variation may be a batch effect from using a constant batch size of 25 fish (Anderson et al. 1994).

The best fitting model (model 1), like competing models 2–4 in Table 4, highlighted two unexpected results. First, it indicated that P decreased with increasing pool depth. This is counterintuitive and runs contrary to our observations that fish were able to jump high waterfalls when taking off from the greatest pool depths. This result may be explained by the fish density (number of fish per liter of plunge pool volume) below the waterfall. It appeared that the motivation for fish to jump was related to fish density. We kept fish numbers constant ($N = 25$), so the lower densities in the deeper plunge pools may have provided less motivation to jump. Tsukamoto et al. (1985) found that the percentage of juvenile ayu *Plecoglossus altivelis* jumping over a waterfall increased with increasing fish density (using batches of 30, 100, and 300 fish) for a fixed plunge pool volume. An alternative explanation is that the inclusion of H_2 in second-order ($H_1 \times H_2$ and $H_2 \times TL$) interaction terms diminished the influence of the first-order H_2 term. This explanation is supported by modeling results that include only the first-order terms (main effects). When analyzing main effects only, the pool depth β estimate is positive (0.007 ± 0.006 ; 95% confidence interval, -0.004 to $+0.02$) instead of negative. Thus, the main-effects model provides weak evidence that P does increase with increasing pool depth if second-order interactions are excluded from the model.

The other surprising result was that P decreased with increasing experiment duration. We expected that P would increase as fish were given more time to ascend the falls. Experimental duration (h) spanned a narrow time range (mean, 22.75; SD 1.42). It is possible that time was confounded by some variable not accounted for in the models. For instance, some fish could have moved downstream once they had entered the upstream compartment. Each of the 440 24-h experiments was videotaped in its entirety. Based on a review of only 6 experiments (by three separate observers), no movement from upstream to downstream was observed. Also,

TABLE 3.—Multiple logistic regression models predicting the probability of a brook trout’s jumping a waterfall of known height (H_1) and plunge pool depth (H_2). Other variables are as follows: C = fish condition, D = trial duration, TL = fish total length, and EBV = extrabinomial variation. Akaike’s information criterion (AIC_c) was used to identify the top four candidate models (based on the lowest AIC_c values, AIC_c values within approximately 3 units of that of the best model, and the highest AIC_c weights) from a set of multiple logistic regression models developed using proc NLMIXED in SAS. The next-to-last column shows the number of estimated parameters (K), the last column the likelihood deviance measure ($\log_e[\mathcal{L}]$) of each model.

Rank	Model	AIC_c	ΔAIC_c	AIC_c weight	K	$\log_e(\mathcal{L})$
1	$H_1 + H_2 + TL + C + D + (H_1 \times H_2) + (H_2 \times TL) + EBV$	5,501.2	0.0	0.41	9	5,483.2
2	$H_1 + H_2 + TL + C + D + (H_1 \times H_2) + EBV$	5,502.7	1.5	0.20	8	5,486.7
3	$H_1 + H_2 + TL + C + D + (H_1 \times H_2) + (TL \times D) + (H_2 \times TL) + EBV$	5,502.8	1.6	0.19	10	5,482.8
4	$H_1 + H_2 + TL + C + (H_1 \times H_2) + EBV$	5,504.4	3.2	0.08	7	5,490.4

during the course of the study, portions of the experiments were observed remotely via television for short periods of time. During such observations, only one fish was observed to jump into the upper compartment successfully and then immediately return downstream, apparently without having swum through the one-way

weir apparatus. The competing models (models 2–4 in Table 4) did not offer evidence contrary to that suggested by model 1 in explaining these unexpected results.

The results from this study suggest that the 1-m standard vertical fall height proposed as a barrier height by the fish migration and passage guide (Evans and

TABLE 4.—Beta estimates (\pm SEs) and 95% confidence intervals for the top four candidate models to predict brook trout jumping success. See Table 3 for additional details.

Variable	β Estimate \pm SE	95% confidence limit	
		Lower	Upper
Model 1			
Intercept	4.80 \pm 1.51	1.84	7.78
H_1	−0.17 \pm 0.016	−0.20	−0.14
H_2	−0.027 \pm 0.025	−0.075	0.021
TL	0.089 \pm 0.032	0.027	0.15
C	−0.48 \pm 0.12	−0.72	−0.25
D	−0.0017 \pm 0.00087	−0.0034	−0.000014
$H_1 \times H_2$	0.0017 \pm 0.00037	0.00097	0.0024
$H_2 \times$ TL	−0.0016 \pm 0.00085	−0.0033	0.00008
EBV	−1.12 \pm 0.077	−1.27	−0.97
Model 2			
Intercept	6.05 \pm 1.38	3.35	8.76
H_1	−0.17 \pm 0.016	−0.20	−0.14
H_2	−0.062 \pm 0.016	−0.094	−0.031
TL	0.034 \pm 0.012	0.01	0.058
C	−0.48 \pm 0.12	−0.72	−0.24
D	−0.0017 \pm 0.00088	−0.0034	0.00003
$H_1 \times H_2$	0.0017 \pm 0.00037	0.00097	0.0024
EBV	−1.15 \pm 0.077	−1.29	−0.99
Model 3			
Intercept	2.71 \pm 0.0028	2.70	2.71
H_1	−0.17 \pm 0.016	−0.20	−0.13
H_2	−0.028 \pm 0.024	−0.075	0.020
TL	0.197 \pm 0.063	0.073	0.32
C	−0.48 \pm 0.12	−0.72	−0.25
D	−0.00016 \pm 0.0007	−0.0016	0.0012
$H_1 \times H_2$	0.0017 \pm 0.00037	0.00099	0.0024
TL \times D	−0.000079 \pm 0.000052	−0.00018	0.00002
$H_2 \times$ TL	−0.0016 \pm 0.00084	−0.0032	0.00007
EBV	−1.12 \pm 0.078	−1.28	−0.97
Model 4			
Intercept	3.81 \pm 0.72	2.39	5.23
H_1	−0.17 \pm 0.016	−0.20	−0.14
H_2	−0.064 \pm 0.016	−0.095	−0.032
TL	0.034 \pm 0.012	0.0097	0.058
C	−0.48 \pm 0.12	−0.71	−0.24
$H_1 \times H_2$	0.0017 \pm 0.00037	0.001	0.0025
EBV	−1.16 \pm 0.078	−1.31	−1.00

TABLE 5.—Predictor variable weights computed as the sum of the AIC_c weights for each predictor variable across all models within the candidate set. See Table 3 for additional details. The most important predictor variables (highest weights) are shown in bold italics.

Variable	Weight
<i>H₁</i>	0.99
<i>H₂</i>	0.99
<i>TL</i>	0.99
<i>C</i>	0.99
<i>D</i>	0.91
<i>H₁ × H₂</i>	0.99
<i>H₁ × TL</i>	0.00
<i>H₁ × C</i>	0.11
<i>H₁ × D</i>	0.04
<i>H₂ × TL</i>	0.72
<i>H₂ × C</i>	0.00
<i>H₂ × D</i>	0.00
<i>TL × C</i>	0.00
<i>TL × D</i>	0.30
<i>C × D</i>	0.00
<i>EBV</i>	0.99

Johnston 1980) is appropriate for brook trout, as we recorded a maximum jump height of 74 cm. Conversely, our results do not agree with either Collins and Elling (1960), who stated that all salmonids could clear a 0.9-m vertical obstacle under laboratory conditions or the predictions of maximum fish jumping heights generated by Aaserude and Orsbom (1985). If we assume that brook trout have jumping capabilities similar to those of coastal cutthroat trout, our top model predicts that a 43-cm brook trout (in good physical condition) attempting to jump over a 1.2-m waterfall from a 60-cm still plunge pool has a 0.05% chance of jumping over the falls within 24 h. This does not agree with Aaserude and Orsbom's theoretical model, which states that a 43-cm cutthroat trout should be able to ascend a 1.22-m waterfall from a still plunge pool. Aaserude and Orsbom also computed that the same

cutthroat trout should be able to ascend a 1.43-m waterfall from a standing wave (generating an upward vertical flow velocity of 0.5 m/s), which would have lower (0.01%) probability of success according to our model. Aaserude and Orsbom's theoretical model results include no measure of the uncertainty associated with their maximum jump height estimates or any statement regarding the pool depth, fish condition, or length of time that a fish has to jump. There are several possible reasons for the differing results between our model and that of Aaserude and Orsbom. First, the hatchery-reared brook trout were not representative of wild brook trout (wild fish may have higher burst swimming speeds than hatchery fish; Duthie 1987). Second, optimal brook trout jumping conditions required us to test deeper plunge pools (optimal pool depth = $1.25 \times$ waterfall height; Stuart 1962). Third, brook trout and cutthroat trout have different sustained or burst swimming speeds and therefore cannot be assumed to be interchangeable. Sustained swimming speed is defined as the velocity that a fish can maintain aerobically for a maximum of 60 min, until it is fatigued. Burst speed is supported anaerobically and is defined as the highest swimming speed maintained for less than 20 s. Tables 6 and 7 show sustained swimming speeds and maximum burst swimming speeds (cm/s) for various salmonids. Fourth, the fish we tested did not exit pools at their maximum burst speed. And fifth, our model does not accurately describe fish jumping capabilities outside the range of total lengths used to generate our models (9–34 cm).

We measured brook trout jumping performance for a limited range of waterfall heights, plunge pool depths, and fish sizes as well as a constant flow of 570 L/min, so we caution against using model 1 as the sole tool for predicting whether existing or proposed drop-structures could be surmounted by this species.

TABLE 6.—Reported sustained swimming speeds (critical swimming velocities) of various salmonids. Unless otherwise specified, fish lengths are fork lengths and error terms are standard errors. Values in brackets are the equivalent speeds (either absolute or relative) calculated from the values reported by the original authors.

Species	Length (cm)	Sustained swimming speed (cm/s)	Relative swimming speed (body lengths/s)	Duration (s)	Reference
Cutthroat trout	8.96 ± 1.2 (SD)	[50]	5.58 ± 0.15	900	Hawkins and Quinn (1996)
Cutthroat trout	8.86 ± 0.8 (SD)	[59]	6.69 ± 0.23	900	Hawkins and Quinn (1996)
Rainbow trout	6–20 (range)	[54 for 10-g fish] [110 for 100-g fish]	9.0 for 10-g fish 5.5 for 100-g fish	60	Fry and Cox (1970)
Rainbow trout (wild)	30.58 ± 1.27 27.5–36.5 (range)	66.57 ± 6.29 47.1–83.2 (range)	[2.2]	600	Jones et al. (1974)
Rainbow trout (hatchery)	32.75 ± 1.2 31.0–34.5 (range)	90.97 ± 2.47 83.3–97.9 (range)	[2.7]	600	Jones et al. (1974)
Rainbow trout	10.01 ± 1.0 (SD)	[77]	7.69 ± 0.17	900	Hawkins and Quinn (1996)
Rainbow trout	8.7 ± 0.1	[52]	6.0	224	Gregory and Wood (1998)
Arctic char <i>Salvelinus alpinus</i>	35.5 ± 1.2	100.2 ± 3.0	[2.8]	600	Jones et al. (1974)
Brook trout	10.6–12.6 (SL; range)	[65–77]	6.17	1,512	Peterson (1974)
Brook trout	10.6–12.6 (SL; range)	[81–96]	7.65	672	Peterson (1974)

TABLE 7.—Values reported for the burst swimming speeds of various salmonids. Unless otherwise specified, reported lengths are total lengths and all values are means ± standard errors.

Species	Length (cm)	Burst swimming speed (cm/s)	Relative swimming speed (body lengths/s)	Duration (s)	Reference
Cutthroat trout	Adult	405			Bell (1986)
Rainbow trout	28.0	270	9.6	1.0	Bainbridge (1960)
	10.3	105	10.2	1.0	Bainbridge (1960)
	14.3 ± 0.4	121	8.5	0.078 ± 0.0004	Webb (1975)
	9.6 ± 0.1	202 ± 10	21	0.071 ± 0.009	Webb (1976)
	15.0 ± 0.7	226 ± 15	15	0.074 ± 0.01	Webb (1976)
	20.4 ± 0.7	214 ± 17	10.5	0.079 ± 0.01	Webb (1976)
	24.5 ± 0.04	229 ± 11	9.3	0.084 ± 0.008	Webb (1976)
	29.6 ± 0.05	191 ± 17	6.5	0.100 ± 0.01	Webb (1976)
	34.6 ± 0.05	203 ± 18	5.9	0.107 ± 0.01	Webb (1976)
	38.7 ± 0.05	265 ± 28	6.8	0.112 ± 0.006	Webb (1976)
	18.4 ± 0.85	132.5 ± 7.3	7.2	0.115 ± 0.007	Webb (1977)
	19.5 ± 0.05	158 ± 21	8.1	0.114	Webb (1978)
	31.6 ± 1.0 (fork length)	277 ± 15	8.7	0.125 ± 0.007	Harper and Blake (1990)
Rinbow Trout (with training protocol)	9.5 ± 0.38 (fork length)	130 ± 7	13.7	0.074	Gamperl et al. (1991)
Rainbow trout (no training protocol)	9.5 ± 0.38 (fork length)	134 ± 14	14.1	0.074	Gamperl et al. (1991)
Brook trout	11.2	93	8.3	10	Peterson (1974)

Other factors that may influence jumping success include variation in flow, water temperature, and the current velocity approaching the crest of the falls (including the landing area). Such factors should not be ignored when incorporating the maximum estimated jumping ability of brook trout into barrier designs. Directed tests of jumping performance using conditions and fish similar to those expected at the site of interest should be conducted.

Based on our results, barriers designed to prevent the upstream movement of brook trout should maintain shallow plunge pool depths (≤10 cm) under a range of flows while achieving the highest vertical drop possible (>100 cm). Specific combinations of waterfall height and plunge pool depth needed to minimize the probability of upstream passage of brook trout can be identified by generating a probability plot based on the top model. Figure 2, an example of such a plot, shows the probability of a healthy, 10 cm brook trout jumping over a waterfall under the physical conditions tested during the laboratory study. If models like ours are applied to field situations, managers need to observe potential barriers under a wide range of flows, particularly those optimal for upstream fish passage.

A recent study by Adams et al. (2000) reported that a 21.0-cm TL brook trout had ascended a 1.2-m-high falls complex comprised of a 0.5-m-high upper step and a 0.7-m-high lower step separated by a plunge pool less than 0.2 m deep. This field report supports our observation that the performance of brook trout under field conditions may exceed that in laboratory tests. It also underscores the importance of evaluating each

“step” of a waterfall complex as a separate jump, because fish may ascend them in stages rather than attempting to clear the whole structure at once.

Our original goal was to derive features for the design of effective barriers to brook trout movement, but it should also be noted that our results are applicable to fish passage issues. If passage of brook trout is the goal, then we would recommend maintaining low vertical heights (<40 cm) and deep plunge

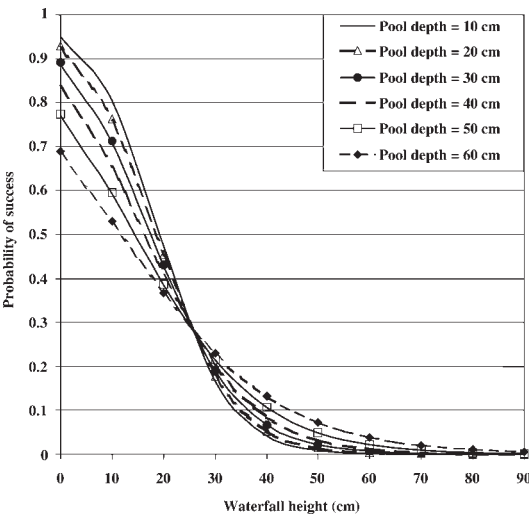


FIGURE 2.—Probability of successfully jumping over a waterfall by a healthy, 10-cm-TL brook trout under the range of waterfall heights and pool depths tested during the laboratory study.

pools. The design of any instream structure will be limited by the local hydrology, geography, and economic realities. However, vertical heights and pool depths should be chosen to exclude as few fish as possible to avoid imposing artificial selection pressures such as selecting for large fish or those that are particularly good jumpers.

Future work should focus on developing fish jumping conditions to allow measurement of maximum jump heights and examination of fish jumping over a wide range of pool depths, experimental trial durations, and flow conditions. The experimental methods developed for this study were specific to brook trout; however, similar techniques should be used to determine the suitability of particular barrier designs or fish passage structures for other riverine species, such as various minnows (Cyprinidae) and suckers (Catostomidae). Fish physiologists can currently measure maximum swimming velocities with reasonable accuracy—the development of equivalent tools and techniques for studying jumping by species other than brook trout would make fish jumping studies more useful.

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References

- Aaserude, R. G., and J. F. Orsborn. 1985. New concepts in fish ladder design. Washington State University, Department of Civil and Environmental Engineering, Final Project Report, Pullman.
- Adams, S. B., C. A. Frissell, and B. E. Rieman. 2000. Movements of nonnative brook trout in relation to stream channel slope. *Transactions of the American Fisheries Society* 129:623–638.
- Anderson, D. R., K. P. Burnham, and G. C. White. 1994. AIC model selection in overdispersed capture–recapture data. *Ecology* 75:1780–1793.
- Bainbridge, R. 1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *Journal of Experimental Biology* 35:109–133.
- Bainbridge, R. 1960. Speed and stamina in three fish. *Journal of Experimental Biology* 37:129–153.
- Baxter, C. V., C. A. Frissell, and F. R. Hauer. 1999. Geomorphology, logging roads, and the distribution of bull trout spawning in a forested river basin: implications for management and conservation. *Transactions of the American Fisheries Society* 128:854–867.
- Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.
- Behnke, R. J., and M. Zarn. 1976. Biology and management of threatened and endangered western trout. U.S. Forest Service General Technical Report RM-28.
- Bell, M. C. 1986. Fisheries handbook of engineering requirements and biological criteria. Fish Passage Development Program, Corps of Engineers, North Pacific Division, Portland, Oregon.
- Burnham, K. P., and D. R. Anderson. 2001. Kullback-Liebler information as a basis for strong inference in ecological studies. *Wildlife Research* 28:111–119.
- Clay, C. H. 1995. Design of fishways and other fish facilities. CRC Press, Boca Raton, Florida.
- Collins, G. B., and C. H. Elling. 1960. Fishway research at the Fisheries-Engineering Research Laboratory. U.S. Fish and Wildlife Service Circular 98.
- De Staso, J., and F. J. Rahel. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. *Transactions of the American Fisheries Society* 123:289–297.
- Dill, W. A., and A. J. Cordone. 1997. History and status of introduced fishes in California, 1871–1996: conclusions. *Fisheries* 22(10):15–18.
- Dimeo, A. 1977. Correcting vertical fish barriers. U.S. Forest Service, Report ED & T 2613, Missoula, Montana.
- Duthie, G. G. 1987. Observations of poor swimming performance among hatchery-reared rainbow trout, *Salmo gairdneri*. *Environmental Biology of Fishes* 18:309–311.
- Evans, W. A., and B. Johnston. 1980. Fish migration and fish passage: a practical guide to solving fish passage problems. U.S. Forest Service, Washington D.C.
- Fausch, K. D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook charr (*Salvelinus fontinalis*) and other resident salmonids in streams? *Physiology and Ecology Japan* 1:303–322.
- Fry, F. E. J., and E. T. Cox. 1970. A relation of size to swimming speed in rainbow trout. *Journal of the Fisheries Research Board of Canada* 27:976–978.
- Gamperl, A. K., D. L. Schnurr, and E. D. Stevens. 1991. Effect of a sprint-training protocol on acceleration performance in rainbow trout (*Salmo gairdneri*). *Canadian Journal of Zoology* 69:578–582.
- Gregory, T. R., and C. M. Wood. 1998. Individual variations and interrelationships between swimming performance, growth rate, and feeding in juvenile rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 55:1583–1590.

- Griffith, J. S. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarkii*) in small streams in northern Idaho. *Journal of the Fisheries Research Board of Canada* 29:265–273.
- Griffith, J. S. 1988. Review of competition between cutthroat trout and other salmonids. Pages 134–140 in R. E. Greswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Bethesda, Maryland.
- Harig, A. L., K. D. Fausch, and M. K. Young. 2000. Factors influencing success of greenback cutthroat trout translocations. *North American Journal of Fisheries Management* 20:994–1004.
- Harper, D. G., and R. W. Blake. 1990. Fast-start performance of rainbow trout *Salmo gairdneri* and northern pike *Esox lucius*. *Journal of Experimental Biology* 150:321–342.
- Hawkins, D. K., and T. P. Quinn. 1996. Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarkii clarkii*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1487–1496.
- Jones, D. R., J. W. Kiceniuk, and O. S. Bamford. 1974. Evaluation of the swimming performance of several fish species from the Mackenzie River. *Journal of the Fisheries Research Board of Canada* 31:1641–1647.
- Kondratieff, M. C., and C. A. Myrick. 2005. Two adjustable waterfalls for evaluating fish jumping performance. *Transactions of the American Fisheries Society* 134:503–508.
- Larson, G. L., and S. E. Moore. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachian Mountains. *Transactions of the American Fisheries Society* 114:195–203.
- MacCrimmon, H. R., and J. S. Campbell. 1969. World distribution of brook trout (*Salvelinus fontinalis*). *Journal of the Fisheries Research Board of Canada* 26:1699–1725.
- Meehan, W. R., and T. C. Bjornn. 1991. Salmonid distribution and life histories. Pages 47–82 in W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Bethesda, Maryland.
- Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions in North American fishes during the past century. *Fisheries* 14(6):22–38.
- Moore, S. E., B. Ridley, and G. L. Larson. 1983. Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. *North American Journal of Fisheries Management* 3:72–80.
- Novinger, D. C., and F. J. Rahel. 2003. Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. *Conservation Biology* 17:772–781.
- Peterson, R. H. 1974. Influence of fenitrothion on swimming velocity of brook trout (*Salvelinus fontinalis*). *Journal of the Fisheries Research Board of Canada* 31:1757–1762.
- Powers, P. D., and J. F. Orsborn. 1985. Analysis of barriers to upstream migration. Washington State University, Department of Civil and Environmental Engineering, Final Project Report, Pullman.
- Reiser, D. W., and R. T. Peacock. 1985. A technique for assessing upstream fish passage problems at small-scale hydropower developments. Pages 423–432 in F. W. Olson, R. G. White, and R. H. Hamre editors. Symposium on small hydropower and fisheries. American Fisheries Society, Bethesda, Maryland.
- Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. *Conservation Biology* 11:1081–1093.
- SAS. 2003 Users's guide, version 8. SAS Institute, Cary, North Carolina.
- Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392–401 in J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.
- Stuart, T. A. 1962. The leaping behavior of salmon and trout at falls and obstructions. Her Majesty's Stationery Office, Freshwater and Salmon Fisheries Research Paper 28, Edinburgh.
- Stuber, R. J., B. D. Rosenlund, and J. R. Bennett. 1988. Greenback cutthroat trout recovery program: management overview. Pages 71–74 in R. E. Greswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Bethesda, Maryland.
- Thompson, P. D., and F. J. Rahel. 1998. Evaluation of artificial barriers in small Rocky Mountain streams for preventing the upstream movement of brook trout. *North American Journal of Fisheries Management* 18:206–210.
- Tsukamoto, K., K. Uchida, Y. Murakami, M. Endo, and T. Kajihara. 1985. Density effect on jumping behavior and swimming upstream in the ayu juveniles. *Bulletin of the Japanese Society of Scientific Fisheries* 51:323.
- Webb, P. W. 1975. Acceleration performance of rainbow trout *Salmo gairdneri* and green sunfish *Lepomis cyanellus*. *Journal of Experimental Biology* 63:451–465.
- Webb, P. W. 1976. The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri* and a consideration of piscivorous predator–prey interactions. *Journal of Experimental Biology* 65:157–177.
- Webb, P. W. 1977. Effects of median fin amputation on fast-start performance of rainbow trout (*Salmo gairdneri*). *Journal of Experimental Biology* 68:123–135.
- Webb, P. W. 1978. Fast-start performance and body form in seven species of teleost fish. *Journal of Experimental Biology* 74:211–226.
- Wiltzius, W. J. 1985. Fish culture and stocking in Colorado, 1879–1978. Colorado Division of Wildlife, Report DOW-R-D-12-85, Fort Collins, Colorado.
- Winston, M. R., C. M. Taylor, and J. Pigg. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. *Transactions of the American Fisheries Society* 120:98–105.
- Young, M. K., R. N. Schmal, T. W. Kohley, and V. G. Leonard. 1996. Conservation status of Colorado River cutthroat trout *Oncorhynchus clarkii pleuriticus*. U.S. Forest Service General Technical Report RM-GTR-282.

ERRATUM

Erratum: How High Can Brook Trout Jump? A Laboratory Evaluation of Brook Trout Jumping Performance

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Page 364. The equation should read as follows:

$$\begin{aligned}\text{Logit}(P) = & 4.81 - 0.17(H_1) - 0.03(H_2) + 0.089(\text{TL}) \\ & - 0.48(C) - 0.0017(D) \\ & + 0.0017(H_1 \times H_2) - 0.0016(H_2 \times \text{TL}) \\ & - 1.12(\text{EBV}).\end{aligned}$$