North American Journal of Fisheries Management 28:231–240, 2008

DOI: 10: 1577/M06-095.1

[Article]

Influences of Body Size and Environmental Factors on Autumn Downstream Migration of Bull Trout in the Boise River, Idaho

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Abstract.—Many fishes migrate extensively through stream networks, yet patterns are commonly described only in terms of the origin and destination of migration (e.g., between natal and feeding habitats). To better understand patterns of migration in bull trout,*Salvelinus confluentus* we studied the influences of body size (total length [TL]) and environmental factors (stream temperature and discharge) on migrations in the Boise River basin, Idaho. During the autumns of 2001–2003, we tracked the downstream migrations of 174 radio-tagged bull trout ranging in size from 21 to 73 cm TL. The results indicated that large bull trout (>30 cm) were more likely than small fish to migrate rapidly downstream after spawning in headwater streams in early autumn. Large bull trout also had a higher probability of arriving at the current terminus of migration in the system, Arrowrock Reservoir. The rate of migration by small bull trout was more variable and individuals were less likely to move into Arrowrock Reservoir. The rate of downstream migration by all fish was slower when stream discharge was greater. Temperature was not associated with the rate of migration. These findings indicate that fish size and environmentally related changes in behavior have important influences on patterns of migration. In a broader context, these results and other recent work suggest, at least in some cases, that commonly used classifications of migratory behavior may not accurately reflect the full range of behaviors and variability among individuals (or life stages) and environmental conditions.

The life cycles of many animals involve migration (Dingle 1996; Secor 2002). Migration is common in salmonid fishes, which are widely recognized for their variable and extensive movements through freshwater and marine habitats (Jonsson and Jonsson 1993; Hendry et al. 2003; Quinn 2005). Traditionally, migratory patterns of salmonids have been defined relative to particular aquatic habitats (e.g., lakes, rivers, estuaries, marine habitats) and direction of movement from natal habitats (e.g., Gresswell et al. 1994; Secor 2002). Such classifications emphasize two key points (i.e., the natal and feeding endpoints) on a continuum of possible destinations. Recent work demonstrates that in many cases a more continuous view may characterize migration more accurately (e.g., Baxter 2002; Meka et al. 2003; Bahr and Shrimpton 2004). Investigations of variability in migratory behavior among individuals may reveal patterns that are much more complex than classifications that focus only on origins and destinations of migration.

We examined factors influencing the downstream movements of bull trout *Salvelinus confluentus*, with a focus on understanding the processes influencing the rate and destination of migrations by individuals of various sizes. Though telemetry studies of large bull trout (>30 cm total length [TL]) are common (e.g., Swanberg 1997; Baxter 2002; Brenkman et al. 2001; Bahr and Shrimpton 2004; Brenkman and Corbett 2005), considerably less work has focused on migration of small (20–30 cm TL) bull trout (Muhlfeld and Marotz 2005). Studies of the latter revealed that small migratory bull trout may use a broader diversity of habitats than found in work done on large fish. We

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Received March 25, 2006; accepted June 21, 2007
Published online February 11, 2008

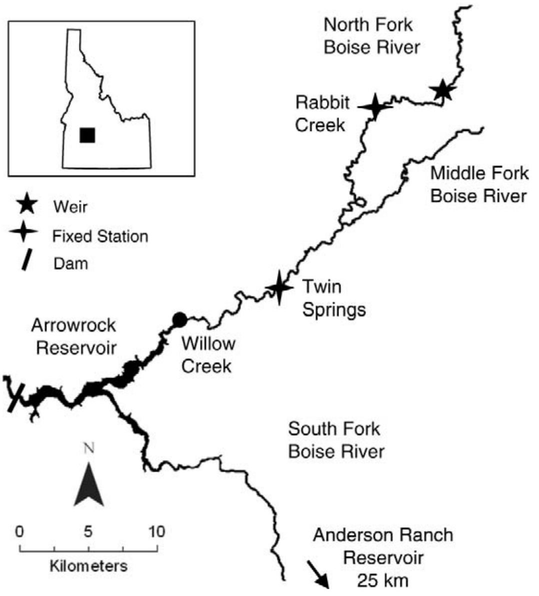

FIGURE 1.—Map of the Boise River basin, Idaho, showing the locations of important sites mentioned in the text. These include the weir where fish were captured and radio-tagged in the North Fork Boise River; Rabbit Creek and Twin Springs, where fixed telemetry receivers were located; and Willow Creek, which marks the upstream end of Arrowrock Reservoir.

hypothesized that body size may be important in determining migratory patterns for several reasons. First, large fish are probably more vulnerable to terrestrial predators in small stream habitats and should benefit from moving to larger or deeper habitats with lower predation risk (Railsback and Harvey 2002). Second, large fish may gain fitness advantages by migrating to habitats with increased productivity or prey availability (Gross et al. 1988; Maekawa and Nakano 2002). Third, large fish may possess prior knowledge of migratory corridors from previous experience (Smith 1985) and thus may be able to navigate more quickly and reliably to downstream destinations. All of these hypothesized size-related influences lead to the common prediction that large bull trout should have a higher probability of migrating to a distant destination and reaching that destination at a faster rate.

In addition to body size (TL), we were also interested in evaluating the potential influences of two other key factors commonly associated with fish migration in river networks: river discharge and water temperature. Changes in discharge and water temperature are commonly associated with migratory movements of bull trout (e.g., Fraley and Shepard 1989; Pratt 1992; Swanberg 1997; Jakober et al. 1998; Brenkman et al. 2001; Muhlfeld and Marotz 2005). Increased river discharge has been linked to increased rates of downstream migration in some juvenile salmon (Irvine and Ward 1989; Whalen et al. 1999), and may similarly facilitate downstream movement by bull trout within size ranges studied herein (Muhlfeld and Marotz 2005). The potential influences of temperature probably depend on the range of ambient conditions within migratory corridors. For example, if temperatures in migratory corridors exceed those causing physiological stress in bull trout (Selong et al. 2001), migration should be less likely or may be delayed (Sauter et al. 2001). Alternatively, if temperatures approach freezing, ice formation and increased vulnerability of fish to endothermic predators (Cunjak 1996) may stimulate downstream migration (Jakober et al. 1998).

To examine these potential influences of body size, river discharge, and water temperature on migration, we tracked the migrations of bull trout through a network of streams bounded on the downstream end by a highly managed reservoir system. This reservoir is considered to be a primary destination for bull trout, which migrate from headwater streams down to the reservoir in autumn (Flatter 2000; Salow 2001). More specifically, our objectives were (1) to predict whether bull trout would migrate into Arrowrock Reservoir during the autumn based on size (TL) and (2) to model the rate of migration into the reservoir as a function of individual size, water temperature, and river discharge.

Study Area

This study was conducted within the upper Boise River basin in southwestern Idaho (Figure 1). Climate in the basin is characterized by cold wet winters and freezing temperatures that contrast with generally hot and dry summers and maximum air temperatures commonly exceeding 30°C. Precipitation is variable, ranging from about 600 to about 1,000 mm/year, a greater proportion falling as snow at higher elevations. This leads to a flow regime with predictably high flows during snowmelt in spring through early summer and low flows during the remainder of the year. Occasional winter or spring storms can produce warm rains on snow that can lead to flooding. Localized flooding can also occur following intense rainfall from convective storms during the warmer months. The autumn period is typically less variable and characterized by lower stream flow than in spring.

Spawning and rearing areas for bull trout are scattered throughout headwater stream systems in the basin (Dunham and Rieman 1999). Bull trout are known to migrate from these headwater habitats to use Arrowrock Reservoir during the autumn, winter, and spring (Flatter

2000; Salow 2001). Fish migrate again upstream in spring and summer into headwater habitats for spawning and to avoid unsuitably warm temperatures in the lower reaches of the watershed, including Arrowrock Reservoir (Flatter 2000; Salow 2001). Arrowrock Dam, which is managed by the U.S. Bureau of Reclamation, represents the farthest downstream habitat available to bull trout (excluding fish that are entrained through the dam itself). The dam creates a reservoir pool volume of up to 3.36×10^5 km^3. The reservoir is managed to maintain a 9.52×10^4-km^3 conservation pool to provide year-round fish habitat. Some bull trout also migrate through Arrowrock Reservoir to use the lower South Fork Boise River, a highly regulated stream segment flowing for 43.5 km downstream from Anderson Ranch Reservoir (Figure 1).

Methods

Fish capture, radio tagging, and tracking.—During the autumns of 2001–2003, downstream migrating bull trout were captured at a weir on the North Fork Boise River (Figure 1). The weir consisted of steel pickets with openings where stream current would guide fish into upstream or downstream trap boxes (Salow 2001). Date of capture, TL (cm), and weight (g) were recorded for each bull trout captured. The capture date of each fish was used as the starting point for each fish's migration time. The location of the weir was downstream from natal habitats ("patches") for bull trout identified in previous work (Dunham and Rieman 1999), and we considered all fish to be migrants by the time they reached the weir.

To determine migration patterns, bull trout were implanted with radio transmitters. The transmitters were digitally coded radio tags with external whip antennae. Tags weighed from 2 to 26 g (Lotek, Newmarket, Ontario, Canada), which ranged from 1.4% to 3.0% of the body weight of tagged fish (Adams et al. 1998). According to manufacturer specifications, tags of this size range were expected to have battery lives ranging from 90 d (2-g tags) to 1,686 d (26-g tags). The surgical method for tag implantation was a modified shielded needle technique (Ross and Kleiner 1982). During surgery, fish were placed ventral side up in a V-shaped surgery cradle. A bilge pump and sprinkler system bathed the gills in an 80-mg/L tricaine methanesulfonate (MS-222) anesthetic solution throughout the surgery. A sterilized tag was inserted into the peritoneal cavity through a small incision (1.0–2.0 cm) made parallel to the mid-ventral line. The antenna exited the body approximately 1.5 cm posterior to the pelvic girdle along the midventral line. The incision was closed with skin staples and surgical glue. After surgery fish were placed in river water to recover for at least 1 h and then released downstream from the weir. In 2002 and 2003, tagged bull trout were held in live wells during daylight hours and released after dark to minimize risk of predation.

Weekly ground and aerial telemetry searches were conducted throughout the autumn migration period to determine movement rates and validate fish survival. Field crews attempted to locate each fish at least once during each week. Ground surveys covered the north shore of Arrowrock Reservoir and the North and Middle Fork Boise River with the exception of a 15-km section of the North Fork Boise River inaccessible by road downstream from Rabbit Creek fixed station (Figure 1). Aerial surveys searched from the weir-capture location downstream to Arrowrock Dam and up the South Fork Boise River to Anderson Ranch Dam (Figure 1). Ground tracking of fish was accomplished by driving and hiking with a radiotelemetry receiver–logger connected to a collapsible three-element Yagi antenna. If fish were suspected mortalities (no movement for more than a week) field personnel conducted in-stream searches for fish or tags by wading and snorkeling as needed. Fish were considered alive until their tag was retrieved or if the radio signal was received from outside of the stream channel. Tracking fish from the air in a fixed-wing aircraft or helicopter involved use of a wing strut or skid-step mounted two-element H-antenna. Flights were conducted within 150 m (helicopter) to 300 m (fixed-wing aircraft) of the river or reservoir. The spatial universal transverse mercator coordinates of located fish were recorded with a hand-held global positioning system. Accuracy of locations was within 1 km during aerial tracking and within 100 m for ground tracking. Coordinates were imported onto topographical maps using National Geographic TOPO! software (San Francisco, California). The software program was used to determine movement distances along the river corridor.

Two fixed telemetry stations were installed to record fish before they moved into areas where radio signals were difficult to receive. A station was placed at the mouth of Rabbit Creek on the North Fork Boise River just upstream from a 15-km steep, roadless canyon and at Twin Springs 9 km upstream from Arrowrock Reservoir (Figure 1). Stations consisted of a four-element Yagi antenna connected to a radiotelemetry receiver–logger powered by a 12-V battery with a solar panel for battery recharge. Date, time, and radio signals were recorded by the logger and periodically downloaded to a laptop computer. The efficiencies of fixed stations were assessed by moving tags on the same and differing frequencies past the station and monitoring recordings on the receiver. We found that stations were able to detect signals from radio tags with an efficiency of more than 95%. Exceptions to this occurred on occasions where multiple tags with synchronized burst rates and timing on the same frequency passed at the exact same time within 3 ft (approximately 1 m) of each other or when electrical interference was encountered. At these times the receiver recorded the tags as error codes; however, they normally were recorded correctly at least once during the time a fish would take to swim past the signal-receiving range of the station.

The location data revealed whether fish remained in the river or entered Arrowrock Reservoir. Reservoir entry occurred on the first day each fish was observed downstream from Willow Creek, located 39 km downstream from the weir where fish were initially captured and tagged (Figure 1). Willow Creek enters the Boise River at the full pool elevation for Arrowrock Reservoir. A fixed station was not installed at Willow Creek for security reasons. When bull trout were found in Arrowrock Reservoir or the South Fork Boise River after more than 7 d without location in the river corridor, a reservoir entry date was estimated by linear interpolation. Calculations used a rate per day based on kilometers traveled between the last date recorded in the river and the first date recorded in the reservoir or South Fork Boise River. To determine a rate we divided the distance from the last river corridor location to the current reservoir or South Fork Boise River location by the number of days the fish was missing. Fish were assumed to have moved at a constant rate for the period of time missing. The rate calculated was then used to estimate the reservoir entry date (kilometers left to travel divided by estimated rate per day). Downstream migration of radio-tagged bull trout was tracked from 12 September to 31 December in all years (2001–2003).

Measurement and estimation of environmental variables.—A Tidbit (Onset Computer Corporation, Pocasset, Massachusetts) data logger at the weir site recorded temperature every 2 h (Figure 1). River discharge (m^3/s) in the Middle Fork Boise River was measured hourly at a gauging station near Twin Springs, Idaho (http://www.usbr.gov/pn/hydromet/webhydarcread.html; Figure 1). Technical difficulties with the sensors, the recorder, or both resulted in missing data values for temperature and river discharge for 1 week in 2001 (river discharge) and 7 weeks in 2003 (water temperature). Water temperature and river discharge for missing data were predicted with simple linear regression models (temperature: $R^2 = 0.99$, $P < 0.0001$; river discharge: $R^2 = 0.89$, $P < 0.0001$) using temperature and river discharge measurements from a nearby gauge station (http://www.usbr.gov/pn/hydromet/webhydarcread.html).

Seven-day averages of temperature and river discharge were chosen to coordinate with the weekly radio-tagged bull trout location interval. Temperature values used for data analysis were the mean daily temperature for 7 d before and after capture for each bull trout that completed migration to Arrowrock Reservoir. The mean river discharge for 7 d after tagging was used for comparisons between environmental conditions and the migration rates of radio-tagged bull trout.

Statistical analysis.—The influence of fish size and capture date on the probability of migration to Arrowrock Reservoir was tested using logistic regression analysis (Allison 1991). Because data were pooled for 3 years, we examined potential differences among year-groups with plots of deviance residuals (Ramsey and Schafer 2002). Standard tests for overdispersion (deviance) and lack of of fit (Hosmer–Lemeshow test) were conducted to ensure a logistic model was appropriate (Allison 1999).

We analyzed the rate of migration in weeks relative to the arrival of fish in Arrowrock Reservoir, a point representing the current downstream terminus of migration in the system. We were unable to identify clear destinations in other portions of the watershed, and focused on Arrowrock Reservoir because of its importance for management of bull trout in the system (Flatter 2000; Salow 2001). Because some fish did not migrate into Arrowrock Reservoir during autumn, we only analyzed those individuals that entered the reservoir. As with probability of entering Arrowrock Reservoir (see previous paragraph), date of tagging of individual fish could be a confounding factor. This was not a significant predictor of migration rate (weeks to entry into Arrowrock Reservoir; unpublished results), however. Accordingly, we focused our analysis only on the effects of fish size, stream temperature, and river discharge on migration rate.

The migration rate was modeled with Poisson regression to predict the number of weeks it took for a fish to travel through the river corridor and enter Arrowrock Reservoir. In a Poisson distribution the variance is equal to the mean (Ramsey and Schafer 2002). Therefore, if the Poisson model fits adequately and the mean time to migrate is longer for small fish than for large fish, the former will also have a higher variance in migration time. Standard diagnostics were examined to assess the fit of a Poisson over alternative models (e.g., overdispersion; Allison 1991).

Results

Bull trout 21–73 cm TL (mean = 38 cm, $n = 174$) were captured and radio-tagged in 2001–2003. Of the 174 bull trout that received radio tags, four radio-tagged fish transmitters were never located due to tag failure or removal from the study area. Twelve radio transmitters were recovered during tracking. These fish were considered mortalities and excluded from the analyses. Of 158 remaining radio-tagged bull trout, 93 traveled to Arrowrock Reservoir during their autumn migration. Downstream migration of radio-tagged bull trout occurred between 18 September and 4 December. Over the 3 years of study, the number of bull trout captured at the weir peaked during the last week of September. By mid-October more than 50% of the radio-tagged fish completed their migration to Arrowrock Reservoir (Figure 2). Logistical, weather, and technical constraints of aerial tracking resulted in a failure to locate only six radio-tagged fish for a period of longer than 7 d. These fish were eventually located in Arrowrock Reservoir or the South Fork Boise River from 10 to 30 d later. Tagged bull trout reached Arrowrock Reservoir each year between 22 September and 14 November (Figure 2). The overall mean time to migrate 42 km from the capture location to Arrowrock Reservoir was 2.8 weeks (95% confidence interval [CI] = 2.4–3.2 weeks), but variability was greater for small fish (see later section).

Probability of Migration

The probability of migration to Arrowrock Reservoir could be predicted from fish length and the day of the year (from 1 January) at time of capture (Table 1). Deviance and Hosmer–Lemeshow goodness-of-fit statistics indicated good fit for this model. Large bull trout were more likely to migrate to Arrowrock Reservoir than small fish (Figure 3; Table 1). Odds ratios indicated that for each centimeter increase in TL there was a 24% increase in the probability of migration to Arrowrock Reservoir (Figure 3; Table 1). Odds ratios showed for each day later in the autumn that fish were tagged, probability of migration to Arrowrock Reservoir decreased by 6% (Table 1).

Rate of Migration

A total of 93 fish migrated into Arrowrock Reservoir, and the rate of migration for these individuals in weeks was predicted as a function of body size and river discharge (Table 2). Deviance values from the Poisson regression showed a good fit for the model and no evidence of overdispersion. Time taken for bull trout to migrate to the reservoir was inversely related to TL of individuals (Figure 4; Table 2). Because small bull trout were less likely to enter Arrowrock Reservoir during autumn than large fish, this analysis included larger-sized fish overall, but small fish were represented in the sample (Figure 4). Whereas the number of weeks to migrate into

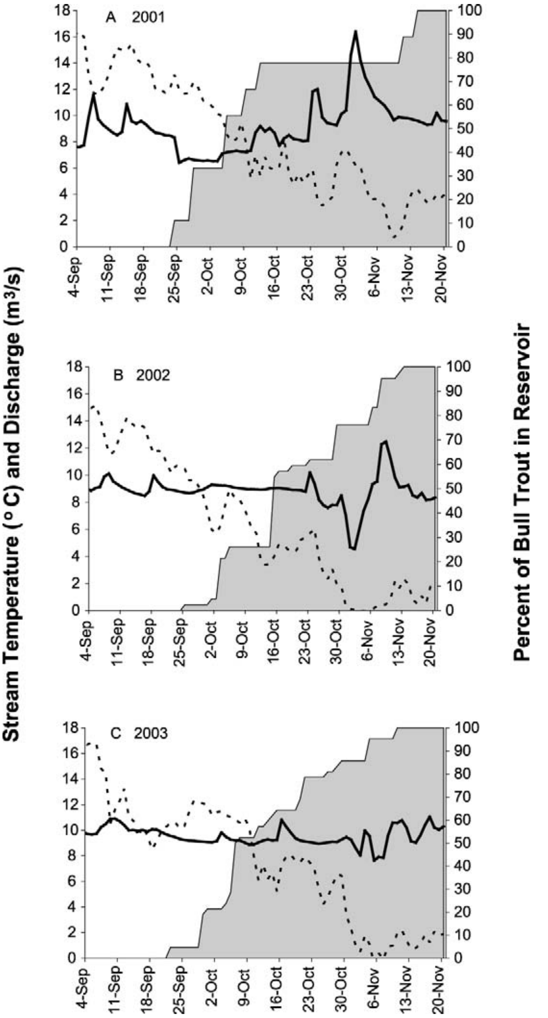

FIGURE 2.—Stream temperatures, river discharges, and the numbers of radio-tagged bull trout present in Arrowrock Reservoir by date in **(a)** 2001 ($n = 9$ fish), **(b)** 2002 ($n = 42$ fish), and **(c)** 2003 ($n = 42$ fish). The dashed lines indicate the mean daily stream temperatures at the capture location. The solid lines indicate the mean daily river discharges recorded at Twin Springs Hydromet Station. The shaded areas indicate the numbers of radio-tagged bull trout present in Arrowrock Reservoir as percentages of all of the bull trout that migrated to the reservoir each year.

Arrowrock Reservoir declined by only 2% for each centimeter increase in TL, there was much higher variability in the rate of migration for small fish (Figure 4). We did not find a significant relationship between rate of migration and stream temperature (Table 2). High mean river discharge for bull trout during the first week after tagging resulted in a slower migration rate to Arrowrock Reservoir. Regression coefficients showed a 45% increase in the predicted number of

TABLE 1.—Results from logistic regression analysis of the effects of fish total length and day of the year (from 1 January) when captured on the probability of bull trout migration to Arrowrock Reservoir (Figure 1) during autumn migrations of 2001–2003.

			95% Confidence limits (Wald's)					
Predictor	β	SE	Lower	Upper	Wald's χ^2	df	*P*	Odds ratio
Intercept	10.49	6.33	−1.92	22.91	2.75	1	0.10	
Total length	0.21	0.04	0.14	0.29	28.29	1	<0.0001	1.24
Capture date	−0.059	0.022	−0.10	−0.02	7.16	1	0.008	0.943

weeks to migrate to Arrowrock Reservoir for each cubic meter per second increase in river discharge (Figure 5; Table 2).

Discussion

The patterns of downstream migration by bull trout were consistent with the predicted influences of body size. Large fish were more likely to migrate to the reservoir and moved downstream at a slightly faster rate than small fish, although the latter showed much more variability in the rate of downstream migration. Stream temperature did not seem to influence the rate of migration, but downstream migration rates decreased as river discharge increased.

Although body size is a good predictor of migratory behaviors, we cannot attribute the effects of body size to a specific mechanism. Experience (Smith 1985) may be an important factor, because large fish are also likely to be older and have a higher probability of completing previous migrations. Tracking fish over longer portions of their life cycle (e.g., from juvenile stages through subsequent spawning attempts) could help to identify individuals with more or less experience with long-distance migration. Other confounding influences of body size may still be a factor, however, including

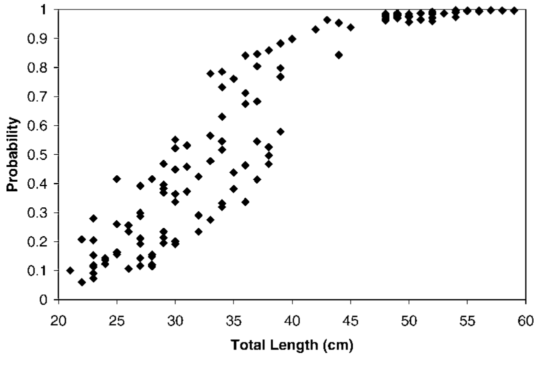

FIGURE 3.—Probability of migration by bull trout ($n = 158$ fish) into Arrowrock Reservoir in relation to TL in the autumns of 2001–2003 as predicted by logistic regression (Table 1).

changes in resource requirements (i.e., food; Gross et al. 1988; Maekawa and Nakano 2002) and size-related strategies to avoid the risk of predation (Railsback and Harvey 2002; Lenormand et al. 2004).

There is some evidence that predation is an important factor in the migratory tendencies in large bull trout, whereas the role of food availability is less clear. Upstream migrations of large bull trout in the Boise River during the early spring and summer are presumably associated with spawning in the autumn (Flatter 2000; Salow 2001). Habitats cold enough to support spawning and early rearing occur primarily above 1,600 m elevation (Dunham and Rieman 1999) and are represented by small headwater streams. Large bull trout in these small systems may be exceptionally vulnerable to avian and mammalian predators (L. Monnot and T. Hoem, personal observations). Predation (including increased vulnerability to human harvest) is commonly noted in studies of migration by bull trout and other *Salvelinus* species (e.g., Swanberg 1997; Beddow et al. 1998; Lenormand et al. 2004; Brenkman and Corbett 2005). In the Boise River, upstream migration by large bull trout into small cold streams, followed by rapid postspawning emigration may represent a trade-off between the benefits of selecting habitats suitable for spawning and early rearing versus the costs of reduced survival from increased predation risk. Our understanding of spatial variability in food resources in the Boise River is lacking, but it may also be possible that large fish migrate rapidly downstream after spawning to recover their depleted energy reserves in habitats with greater food availability.

Our observation that the rates of migration by bull trout slow as river discharge increases may also be interpreted as reflecting the influences of predators or perceived predation risk. Greater river discharge is associated with increased availability of deeper water, increased turbulence, and decreased underwater visibility, all of which may reduce the threat of predation. Other behaviors of bull trout during autumn and winter suggest that predator avoidance is an important factor.

TABLE 2.—Results from Poisson regression analysis of the rate of migration (number of weeks required) for bull trout to reach Arrowrock Reservoir (Figure 1) in relation to total length, water temperature, and river discharge during the autumn migrations of 2001–2003.

Predictor	β	SE	95% Confidence limits (Wald's) Lower	Upper	Wald's χ^2	df	*P*
Intercept	−1.73	0.98	−3.66	0.20	3.09	1	0.08
Total length	−0.02	0.006	−0.04	−0.01	15.99	1	<0.0001
Temperature	0.04	0.03	−0.02	0.10	1.88	1	0.17
Discharge	0.37	0.11	0.16	0.58	11.84	1	0.0006

For example, bull trout are more likely to use cover when temperatures decline (concealing themselves in substrate [Thurow 1997] and deeper water [Jakober et al. 1998]) and to shift to more nocturnal behavior (Baxter and McPhail, 1997; Goetz 1997; Jakober et al. 2000; Muhlfeld et al. 2003), both of which may reduce the risk of predation by birds or mammals (Cunjak 1996). Evidence of a link between increasing river discharge, additional cover due to increased turbidity, and slower migratory rates have also been found in Chinook salmon *Oncorhynchus tshawytscha* (Gregory and Northcote 1993; Gregory and Levings 1998) and brown trout *Salmo trutta* (Bohlin et al. 1993). It is also possible that increases in river discharge could temporarily increase availability of drifting macroinvertebrate prey (e.g., Bond and Downes 2003), and fish may slow their rate of movement to exploit this ephemeral resource.

Water temperature was not associated with the rate of downstream migration of bull trout. This may be due to the fact that observed water temperatures were moderate relative to the physiological requirements of bull trout (Selong et al. 2001). Cessation of downstream migratory activity and arrival of bull trout in Arrowrock Reservoir during autumn appeared to occur in late November to early December, as water temperatures consistently approached freezing conditions. Similar patterns were observed for the downstream migrations of brook trout *Salvelinus fontinalis* in relation to freezing temperatures (Curry et al. 2002). In contrast, bull trout in coastal areas experiencing more temperate winters have been observed to migrate downstream well into the winter (Brenkman and Corbett 2005).

We did not view the effect of size on the mean rate of migration to be biologically significant, but the higher variability in the rate of migration that we observed for small bull trout may be important. This result suggests that many small fish make extensive use of habitats considered to serve mostly as migratory corridors for large fish. Many small fish did not leave these corridors during the autumn. It would be instructive to study habitat use by small bull trout in this system over the duration of the winter (e.g., Muhlfeld and Marotz 2005), but the smaller tag size (and shorter battery life) needed for small bull trout and the limited access to habitats for tagging additional fish in winter were important constraints in the system we studied. Despite these limitations, our results parallel

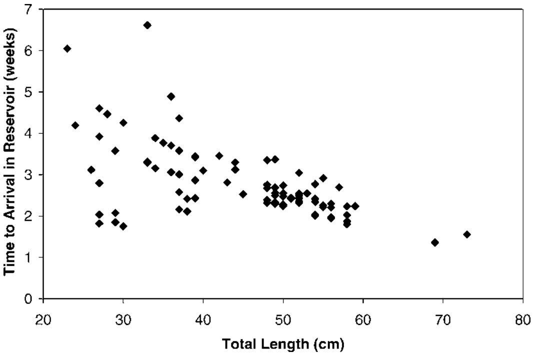

FIGURE 4.—Number of weeks required for downstream-migrating bull trout of various sizes ($n = 93$ fish) to reach Arrowrock Reservoir during the autumns of 2001–2003 as predicted by Poisson regression (Table 2).

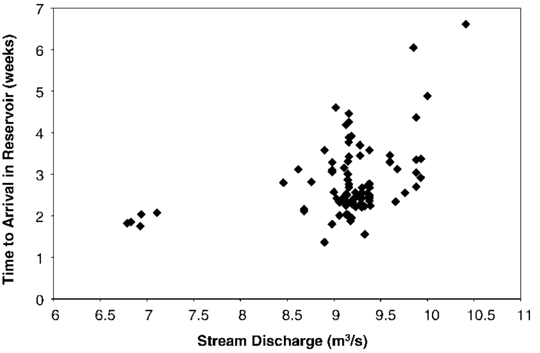

FIGURE 5.—Number of weeks required for downstream-migrating bull trout ($n = 93$ fish) to reach Arrowrock Reservoir at various discharges during the autumns of 2001–2003 as predicted by Poisson regression (Table 2).

those of Muhlfeld and Marotz (2005) in that small migratory bull trout have substantially different behaviors than large individuals.

Finally, whereas our results indicate that small fish spend more time in riverine habitats than large fish, there may also be important parallels in the spatial patterns of habitat use. In the Boise River, small migratory bull trout have been captured in many tributary habitats considered too small or thermally unsuitable on a year-round basis to support spawning and early rearing (L. Monnot, T. Hoem, and J. Dunham, personal observations). This indicates that tracking individual movements may not reveal such patterns of habitat use, even with a relatively large sample size (>100 individuals). It may also be that such behaviors are not frequent enough to be reliably detected by weekly monitoring of fish locations. Furthermore, many of our observations of fish in these small streams occurred outside of the time of year that fish were tracked in this study. In most stream networks where bull trout presently occur, there are vast areas of such habitats that are potentially accessible. Future work focusing more on these spatial patterns of use would be needed for a complete understanding of the relevance of these habitats for bull trout. Collectively, these observations indicate that habitat requirements for small migratory bull trout are much more extensive than would be revealed by a study of large fish alone, paralleling similar work in other systems (Muhlfeld and Marotz 2005).

Our work supports the growing contention that the migration of stream fishes is much more complex than studies focusing on the points of origin and ultimate destination indicate (Secor 2002). The "restricted movement paradigm" has been extensively reexamined in the literature on nonmigratory salmonids over the past decade or so (e.g., Gowan et al. 1994; Rodríguez 2002). We see a similar reexamination taking place with respect to the migratory behavior of salmonids. In particular, it is becoming apparent that migration depends strongly on the size, age, or life stage of the fish as well as on the nature of the stream networks in which they occur (i.e., the connectivity of streams to various habitats and the spatiotemporal variation in habitat conditions; Schlosser 1991). We anticipate that the view of migration will continue to evolve in concert with the availability of technologies for continuously tracking more individuals at more life stages in more habitats.

Acknowledgments

This work was funded by the U.S. Bureau of Reclamation, Snake River Office West, and was a cooperative effort with Boise National Forest and Idaho Department of Fish and Game. Thanks are extended to Joe Chigbrow, Darren Cross, Matthew Dare, Jeff Dillon, Steve Dunn, Gretchen Fitzgerald, Brian Flatter, Amber Fonner, Michael Kellett, Rick Rieber, Josh Royse, Carl Stiefel, and Scott Vuono for field assistance. Laura Bond from Boise State University provided statistical guidance. Mark Fuller from the U.S. Geological Survey Forest and Rangeland Ecosystem Science Center provided important support and perspective throughout the project. Sam Brenkman, Doug Bateman, and two anonymous reviewers provided constructive criticisms on an earlier draft of this manuscript. Use of trade or firm names is for reader information only and does not imply endorsement of any product or service by the U.S. Government.

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