

Temporal and Spatial Variability in the Migration Patterns of Juvenile and Subadult Bull Trout in Northeastern Oregon

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Abstract.—Conservation planning for threatened bull trout *Salvelinus confluentus* requires the identification of temporal and spatial movement patterns to better understand the patch size and connectivity requirements of different behavioral strategies (e.g., resident and migratory) and life stages (e.g., juvenile and adult). Although these patterns have been identified for adults, less is known about the movement patterns of juvenile and subadult bull trout. Thus, we evaluated the movement patterns and abiotic and biotic cues associated with migration timing of fluvial juvenile and subadult (150–300 mm) bull trout in the South Fork Walla Walla River, northeastern Oregon. From 2002 to 2005, we tagged 1,636 individuals with passive integrated transponder (PIT) tags and monitored subsequent movements (within the study area) and migrations (exiting of the study area) by PIT tag detection at antennae and active detection during the mark-recapture sampling season. Juveniles and subadults exhibited downstream movements and migrations throughout the year; movement and migration activity peaked in August, and migrations occurred predominantly at night (94%). We modeled migration timing in response to abiotic and biotic cues and observed distinct seasonal patterns in migration timing that were associated with changes in minimum temperature. However, the seasonal models based on temperature explained only 23–35% of the variation in migration timing, suggesting the influence of additional variables. Based on the temporal and spatial continuum of movement observed here, we believe that management must address the occupancy of multiple habitat types and migration corridors throughout the year.

In an environment characterized by instability or degradation, fish populations that contain both resident and migratory individuals are better able to persist in the face of change (Northcote 1992; Lichatowich 1999). These life history strategies are of particular importance, as they represent evolutionary diversity that has allowed fish to adapt to and take advantage of various resources in the environment (Dingle 1996). Furthermore, these strategies can be negatively affected by changes to the environment (Schlosser 1991; Quinn and Adams 1996). For imperiled species in particular, it is critical to determine the patch size and connectivity requirements associated with multiple behavioral strategies. For example, highly mobile anadromous sockeye salmon *Oncorhynchus nerka* can move distances greater than 900 km while utilizing disparate habitat patches and migratory corridors, whereas kokanee (lacustrine sockeye salmon) can spend their entire life cycle in a single lake (Groot and Margolis 1991). Ultimately, these diverse life history forms may be important to population persistence because they (1)

disperse population-level mortality risk via occupation of multiple habitat patches through time, (2) facilitate gene flow, and (3) can reestablish populations in unoccupied habitat patches (Gross 1991; Jackson et al. 2001).

The migration patterns of salmonids have been widely studied. Historic migration patterns of Pacific salmon are believed to have occurred on a spatial and temporal continuum before populations were severely exploited and before impoundments altered flow regimes and decreased connectivity (Lichatowich 1999). In contrast, current Pacific salmon migrations tend to occur during discrete time periods (e.g., seasons) and are stock specific (e.g., spring Chinook salmon *O. tshawytscha*), and the duration of the migration is related to the specific strategy employed (fluvial, adfluvial, or anadromous; Groot and Margolis 1991). Other salmonids (e.g., chars *Salvelinus* spp.: Nordeng 1983; cutthroat trout *O. clarkii*: Schrank and Rahel 2004) demonstrate migration patterns that are much more variable in timing and distance. In addition, these fish may switch seasonally or annually from a migratory tactic to a resident one (Hilderbrand and Kershner 2000; McDowall 2001).

Salmonids respond to different migration cues across

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life stages and geographic regions. Temperature is associated with the downstream dispersal of smolts (Whalen et al. 1999) and with spring and fall migrations (Swanberg 1997; Jonsson and Jonsson 2002), while discharge is associated with migration timing for multiple life stages (Quinn and Adams 1996; Downs et al. 2006). The seasonal and diel timing of smoltification (Thorpe and Morgan 1978; McCormick et al. 1998; Byrne et al. 2003) and migration (McCormick et al. 1998; Riley et al. 2002; Muhlfeld et al. 2003) is associated with photoperiod. Salow (2005) alluded to the possibility that precipitation provides a cue for migration. The evidence for a diverse array of migration cues illustrates how environmental variability or heterogeneity may result in differential migration responses across the range of a species or between species.

Bull trout *Salvelinus confluentus* are native to the Pacific Northwest and exhibit a complex array of migration patterns. Throughout their range, bull trout co-occur in resident and migratory forms (Rieman and McIntyre 1993). Adult resident fish may be 150–300 mm total length (TL), while adult migratory fish may grow to well over 600 mm (Fraley and Shepard 1989). Bull trout require cold, clean water and have been associated with complex habitat (Rieman and McIntyre 1993). Many factors (e.g., habitat degradation, fragmentation, and migration barriers) have contributed to rangewide declines, particularly for the migratory form, and the species is listed as threatened under the U.S. Endangered Species Act (USFWS 1999; Nelson et al. 2002).

Adult bull trout exhibit migrations across broad temporal and spatial scales (up to 250 km; Fraley and Shepard 1989; Swanberg 1997; Baxter 2002) and in association with many cues. Both adfluvial and fluvial adults typically initiate spawning migrations to natal streams in the late spring or summer as temperatures approach 10–12°C and as the hydrograph decreases (Goetz 1989; Elle and Thurow 1994). The fish then migrate out of the system (postspawn period) as temperatures decrease in the fall (Fraley and Shepard 1989; Flatter 2000; Hostettler 2004). Some adults may hold over in the natal stream and emigrate during the subsequent spring (K. Homel, personal observation), but in general little migration is observed during the winter unless anchor ice or harsh river conditions displace the fish (Jakober et al. 1998; Hostettler 2003). Overall, adult bull trout migrations tend to occur over discrete time periods that vary across basins (Fraley and Shepard 1989; Swanberg 1997).

In contrast to adult migration patterns, juvenile and subadult migration patterns are not as well understood and cues for migration have not been formally tested.

Most bull trout migrate at age 2, although some age-1 and age-3 fish also migrate (Pratt 1992). The distance and rate of migrations vary considerably both with body size (Hostettler 2004) and seasonal changes in discharge or temperature (Salow 2005; Downs et al. 2006). In addition, these variables can affect migration of young-of-year and juvenile fish differentially (Downs et al. 2006). As the migratory life history form is of particular conservation importance, it is critical to identify (1) the role of migratory cues in determining life history characteristics and (2) the subsequent effects of altering those cues on survival and population demographics.

Our goal was to evaluate the downstream migration patterns of fluvial juvenile and subadult bull trout (120–300 mm TL) to better understand the migration time frame and distance and the potential migration cues. Although the distinction between migration and movement is important and has been discussed extensively (Dingle 1996), it is not the focus of this research. Therefore, for the purpose of this study, we define migratory movements (hereafter, migration) as annual downstream movements between distinct habitat types and we define diel and seasonal movements (hereafter, movement) as upstream or downstream movements within the same habitat type. We combined active mark–recapture techniques with passive integrated transponder (PIT) tag detection at instream antennae to (1) monitor the daily and seasonal movements of juvenile and subadult bull trout, (2) determine the timing of downstream migration, and (3) identify potential cues that may prompt this migration.

Methods

Study area.—The South Fork Walla Walla River (SFWWR) is a snowmelt-dominated second-order stream in northeastern Oregon (Figure 1). Bear, Skiphorton, and Reser creeks are the major tributaries of the SFWWR, and most observed spawning activity occurs in proximity to these tributaries. Within the SFWWR, the habitat is generally of high quality and is subject to limited recreational activity (particularly in the headwaters). Downstream of the confluence with the North Fork Walla Walla River, the habitat conditions become degraded, as evidenced by increased water temperature, simplified channel and habitat, presence of impoundments, and depletion of flow by irrigation withdrawals.

Study design.—This work was part of a larger research effort aimed at creating a general template for recovery planning of bull trout across the species' range (Al-Chokhachy et al. 2005; Al-Chokhachy 2006; Homel 2007). Within the larger effort, we conducted a mark–recapture–resight study to evaluate population

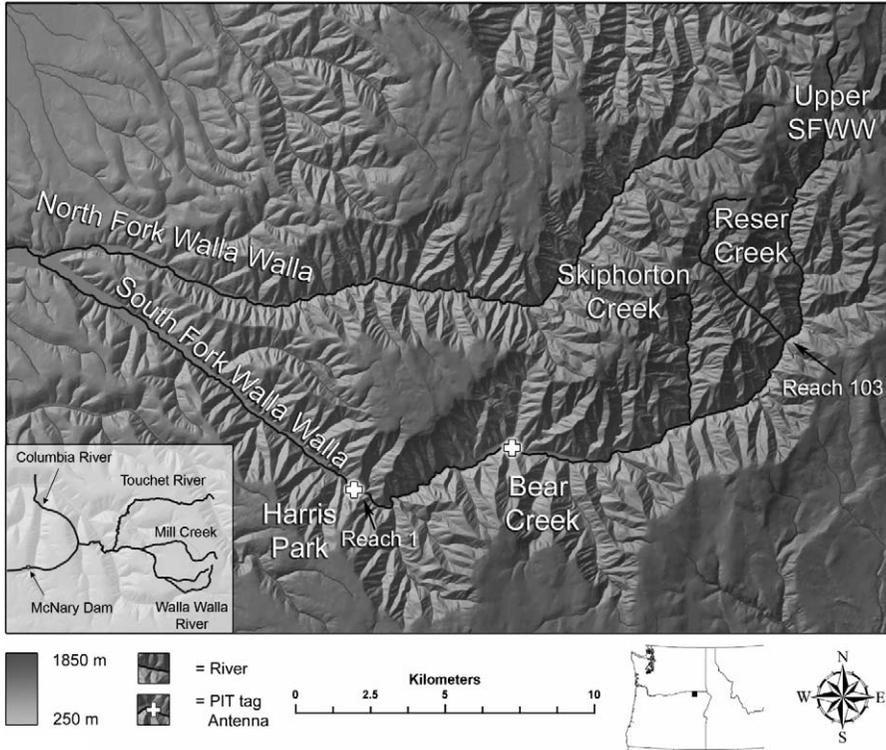


FIGURE 1.—Map of the South Fork Walla Walla River (SFWR) study area, Oregon, showing locations of antennae used to monitor movements and migrations of passive integrated transponder (PIT) tagged juvenile and subadult bull trout.

size and structure. For the current study, we continued a mark–recapture sampling design described by Al-Chokhachy et al. (in press) and summarized briefly here. We set the lower bound of our study site at Harris County Park and the upper bound 21 km upstream at Reser Creek (Figure 1); the study site was then divided into 103 adjacent reaches of approximately 200 m each. During each study year (2002–2005), we systematically sampled 20 equidistant index reaches and an additional 20 variable reaches (Al-Chokhachy et al., in press). By systematically sampling the entire study area, we were able to account for spatial heterogeneity in the distribution of bull trout and monitor the migrations originating throughout the study area.

Fish capture and marking.—To avoid size bias in our sampling, we used multiple techniques to capture fish, including backpack electrofishing downstream to a seine, trapnetting, use of baited minnow traps, angling, and snorkeling to a seine. All active sampling occurred during summer base flow conditions (June–August). Captured bull trout were weighed, measured, and scanned for PIT tags. Fish exceeding 120 mm TL were anesthetized in a solution of tricaine methanesul-

fonate (MS-222). Once a fish became unresponsive to stimuli, we made a 3-mm ventral incision, implanted a 23-mm PIT tag into the body cavity, and marked the fish externally with a Floy tag for mark–resight analysis (Al-Chokhachy et al. 2005). After implantation, fish were held in a flow-through recovery tank until full equilibrium was restored. We released fish in slow water close to the point of capture.

Quantification of movement and migration.—From 2003 to 2005, we used both active mark–recapture sampling and PIT tag detection at fixed antennae to monitor upstream and downstream fish movements that occurred within the study area and downstream migrations of juveniles and subadults exiting the study area. In 2002, we installed two antennae in the SFWR (Harris Park and Bear Creek sites; Figure 1) to record the date, time, and individual tag number of marked fish that passed through the antenna loop. The antenna at Harris Park was located at the major transition in habitat quality described above. According to a definition of migration based on a functional shift in habitat quality, fish moving downstream of this antenna would be considered migratory. The antenna at Bear Creek was located 7 km upstream of Harris Park

and was used to quantify diel and seasonal movement occurring within our study area. We inferred upstream and downstream movement direction for all individuals that swam through both antennae; movement direction was also inferred for fish that swam through a single antenna after active capture. For example, if a fish was captured and tagged in reach 78 and subsequently detected at the Bear Creek antenna (reach 37), then we inferred a downstream movement. Detections of individual fish were the basis for (1) quantifying movement within the study area, (2) determining which component of the population was migratory (i.e., migrated downstream past the Harris Park antenna to exit the study area), and (3) establishing the time frame and distance over which migration occurred. In addition, although not explicitly part of this study, three other PIT tag antennae were located further downstream from our study area (Nursery Bridge Dam on the Walla Walla River, 24 km below Harris Park; Touchet River; and Mill Creek) and allowed for detection of fish that migrated even further downstream.

Abiotic and biotic variables.—Abiotic and biotic variables that could serve as potential cues for migration were measured primarily at the Harris Park antenna on the SFWWR. We collected hourly stream temperature from 2004 to 2005 based on data from a gauging station at the Harris Park site. We obtained daily precipitation and photoperiod data from local gauging stations (U.S. Department of Agriculture, High Ridge Snow Telemetry site) and conducted instream validation of photoperiod with a Licor light meter. Here, we define daytime as the hours of visible light (approximately 1 h before sunrise to 1 h after sunset). Next, we measured stream discharge at the Harris Park site in 2004 and 2005 using a Marsh-McBirney FloMate flowmeter; this information corroborated gauge height measurements that were recorded electronically and continuously at the same site. Finally, we examined the presence of spawning adults as a potential cue for migration. By active sampling and passive detection at antennae, we monitored the upstream and downstream migrations of previously tagged large fish in our system to determine the time frame in which they could potentially influence juvenile and subadult migration timing.

Data analysis.—We evaluated several aspects of movement and migration in the SFWWR. First, we assessed diel, seasonal, and annual movement timing of bull trout within the study area. We summarized both upstream and downstream movements based on all passive detections of fish (2003–2005) at the Bear Creek and Harris Park antennae. We used mark-recapture detections to further define movement

direction for fish that only passed through a single antenna.

Detection efficiency at passive antennae is a complex function of (1) antenna efficiency, or the ability of the antennae to detect a tagged fish and (2) the occurrence of temporary time periods when antennae are inoperable due to uncontrollable events (Zydlewski et al. 2006). Previously, the U.S. Fish and Wildlife Service (Columbia River Fisheries Program Office, unpublished data) estimated antenna efficiency at the Harris Park site to be 80–100% (i.e., this is the percentage of tags passing through the antenna loop that were detected; the range in detection is influenced by environmental conditions). Given this high level of antenna efficiency, we were more concerned with the frequency of antenna operation. We assessed the operating frequency based on (1) the known number of missed detections and (2) periods of inoperability. Because we had multiple antennae and multiple active sampling recapture events, we knew which fish had traveled out of the study area and returned. If a fish was detected at the uppermost antenna (Bear Creek) and then detected months later at Nursery Bridge Dam but not at Harris Park (located between the other two sites), a missed detection at the Harris Park antenna was therefore indicated. Periods of known missed detections at Harris Park corresponded with periods of power outages that caused antennae to be inoperable. As such, we summed the total number of hours of Harris Park antenna inoperability and divided it by the total number of hours encompassed by our multiyear study to estimate daily antenna efficiency. From 2003 to 2005, this calculation of antenna efficiency was highly variable (50–100%). Therefore, to capture all potential cues for migration timing across a yearly cycle, we used a subset of our detection data from a period of nearly continuous antenna operation for formal statistical evaluation of downstream migration cues and timing for bull trout exiting the study area at Harris Park. Data collected from September 1, 2004, to December 31, 2005, were used for statistical models, as consistently high detection efficiency (80–100%) was observed for this period.

We considered a set of 12 a priori candidate models based on biological hypotheses of factors influencing annual migration timing in other populations of bull trout or other species. Using linear regression techniques in the Statistical Analysis System (version 9.1; SAS Institute 2002), we quantified the number of migrants per unit time (10 d) in response to the following combinations of abiotic and biotic variables and their interactions: (1) minimum temperature, (2) maximum temperature, (3) discharge, (4) precipitation, (5) photoperiod, (6) number of upstream-migrating

TABLE 1.—Summary of five highest-ranked annual models and highest-ranked seasonal models describing the influence of abiotic and biotic variables on the number of passive integrated transponder tagged juvenile and subadult bull trout detected as migrating past fixed antennae on the South Fork Walla Walla River, northeastern Oregon, during each 10-d period in 2003–2005 (N = sample size; T_{\min} = minimum temperature, °C; Q = gauge height, m; precip = precipitation, cm; adults = number of upstream-migrating adult bull trout; adj. R^2 = adjusted coefficient of determination). For each model, the slope (β) from the regression equation is reported for the included explanatory variables; dashes indicate variables that were excluded from a model. Ranks were based on Akaike's information criterion (AIC); the AIC difference (Δ AIC) between each model and the best model (i.e., that with the lowest AIC) is also shown. For the seasonal models, sample sizes varied among seasons, so AIC scores were comparable only within a season.

Model	N	Intercept	β				Model statistics				
			T_{\min}	Q	Precip	Adults	P	F	Adj. R^2	AIC	Δ AIC
Annual											
1	54	0.42	0.07	-	-	-	0.11	2.6	0.03	-41.98	0.00
2	54	0.3	0.09	-	-	-0.11	0.13	2.11	0.04	-41.65	0.33
3	54	-670.79	0.08	0.34	-	-	0.22	1.58	0.02	-40.59	1.39
4	54	0.9	-	-	-0.51	-	0.34	0.94	0.00	-40.32	1.66
5	54	0.5	0.06	-	-0.26	-	0.26	1.39	0.02	-40.22	1.76
Seasonal											
Fall	23	3,748.23	0.22	1.9	-	-	0.02	4.88	0.31	-18.00	
Winter	4	1.62	-0.32	-	-	-	0.06	5.02	0.31	-17.13	
Spring	10	2.87	-0.29	-	-	-	0.05	5.31	0.35	-12.40	
Summer	17	-4.01	0.64	-	-	-0.22	0.13	2.61	0.23	-7.59	

adult bull trout, (7) a global model that included all variables except maximum temperature, (8) discharge and the minimum temperature \times photoperiod interaction, (9) discharge \times precipitation interaction, (10) minimum temperature and precipitation, (11) minimum temperature and discharge, and (12) minimum temperature and number of adult upstream migrants. We ranked these 12 annual models according to Akaike's information criterion (AIC; Burnham and Anderson 2002) and selected the five highest-ranked models (i.e., those that had the lowest AIC scores; Table 1). We then evaluated seasonal models of migration timing and cues (using variables from the five highest-ranked annual models) and selected the highest-ranked model for each season based on AIC scores. Due to unequal sample sizes across seasons, seasonal models were only compared with other models describing the same season (e.g., each winter model was compared with only winter models; Table 1).

Results

Movement Patterns within the Study Area

Over the course of our study, we detected a large degree of movement within the bull trout population and recaptured fish up to 14 km from the initial tagging location. During 2002–2005, we PIT-tagged 1,636 bull trout (120–720 mm TL); from 2003 to 2005, the Bear Creek and Harris Park antennae recorded 938 fish detections. At Harris Park, most (94%) of the downstream migration detections for all size-classes occurred at night (nighttime detections = 143; daytime detections = 9). Juveniles and subadults (120–300 mm TL on the tagging date) accounted for 1,312 of the

tagged fish and 539 of the detections of fish moving upstream or downstream past the Bear Creek and Harris Park antennae; these detections occurred throughout the entire year (Figure 2). Of the 286 juvenile and subadult detections at Bear Creek, 37%

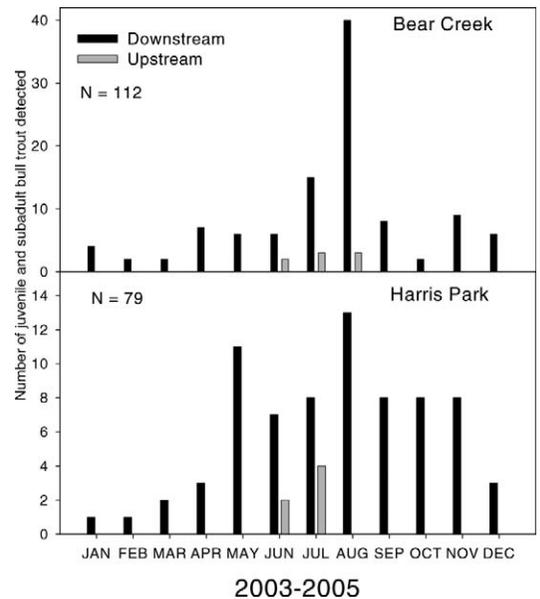


FIGURE 2.—Monthly detections of upstream (gray bars) and downstream (black bars) movements made by passive integrated transponder-tagged juvenile and subadult bull trout (120–300 mm total length) at two stationary antennae (Bear Creek and Harris Park; the y-axis scale differs between sites) on the South Fork Walla Walla River, northeastern Oregon, 2003–2005.

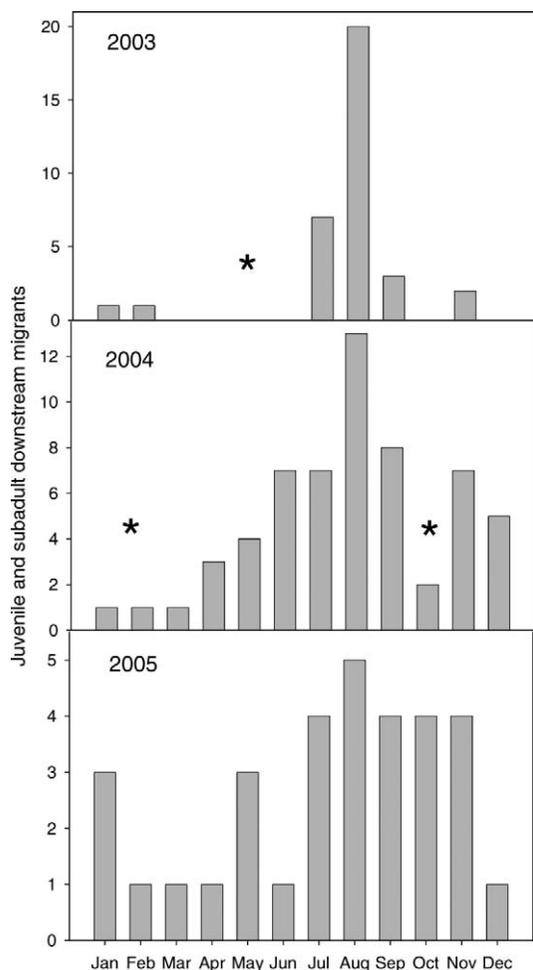


FIGURE 3.—Downstream migration timing of passive integrated transponder-tagged juvenile and subadult bull trout (120–300 mm total length) detected at stationary antennae (Bear Creek and Harris Park) on the South Fork Walla Walla River, northeastern Oregon, 2003–2005 (the y-axis scale differs among years). Asterisks indicate periods in which an antenna was inoperable or was operating at low (<50%) efficiency. Because of variable detection in 2004 at Harris Park (the downstream antenna, used to detect fish exiting the study area), movement direction could not be identified for many of the fish that were detected at only one antenna in 2005.

were of downstream movement, 2% were of upstream movement, 53% were repeat detections of stationary fish, and 8% could not be assigned a movement direction (Figure 2). Of the 253 juvenile and subadult detections at Harris Park, 29% were of downstream movement, 2% were of upstream movement, 65% were repeat detections of stationary fish, and 4% could not be assigned a movement direction (Figure 2). Of the

180 juvenile and subadult fish detected as moving downstream, 74 exited the study area at Harris Park and were therefore considered migratory.

Downstream Migration Timing and Distance

Bull trout exhibited temporal and spatial variation in downstream migration patterns. Juveniles and subadults migrated downstream past the Harris Park antenna throughout the entire year; an initial downstream pulse of migrants was detected in the spring, and a larger pulse was detected in August (Figure 3). In addition, 10 juveniles and subadults were detected at Nursery Bridge Dam (Figure 1) in January and February. None of the bull trout marked in the SFWWR was detected at any antenna on the Columbia River or on other tributaries to the Walla Walla River (e.g., Mill Creek and Touchet River). A fish from the SFWWR would have to migrate 127 km to be detected at a Columbia River antenna.

Abiotic and Biotic Variables

During 2002–2005, abiotic and biotic variables differed across years; however, for illustration, we report variables measured from September 2004 to December 2005, which corresponds to period used for modeling of migration timing. Maximum water temperature in the study area was 15.25°C, and minimum temperature approached 1.00°C (Figure 4). Flows peaked in the late spring (gauge height = 602.07 m [1,975.3 ft], corresponding to a flow of ~4.25 m³/s [150 ft³/s]) concurrent with snowmelt runoff and peaked again in December (602.13 m [1,975.5 ft]) in response to precipitation (Figure 4). The SFWWR received 86.86 cm of precipitation (primarily in March–April) in 2005 (Figure 4). From 2003 to 2005, we observed consistent patterns of adult migration; adults moved upstream into the study area in May and June and exhibited postspawn downstream movements in September (Figure 5). During the modeled period of migration timing, we detected 20 tagged adults migrating upstream primarily in June and July but more untagged adults were known to have migrated upstream based on spawner counts and active sampling (Al-Chokhachy et al. 2005; Al-Chokhachy 2006; Homel 2007).

Influence of Cues on Migration

We modeled the migration timing of 54 juveniles and subadults from September 1, 2004, to December 31, 2005; although migration varied seasonally, it could not be predicted solely from environmental and biological cues. Of the 12 models tested, the five highest-ranked models were not significantly different from each other according to AIC. Our most

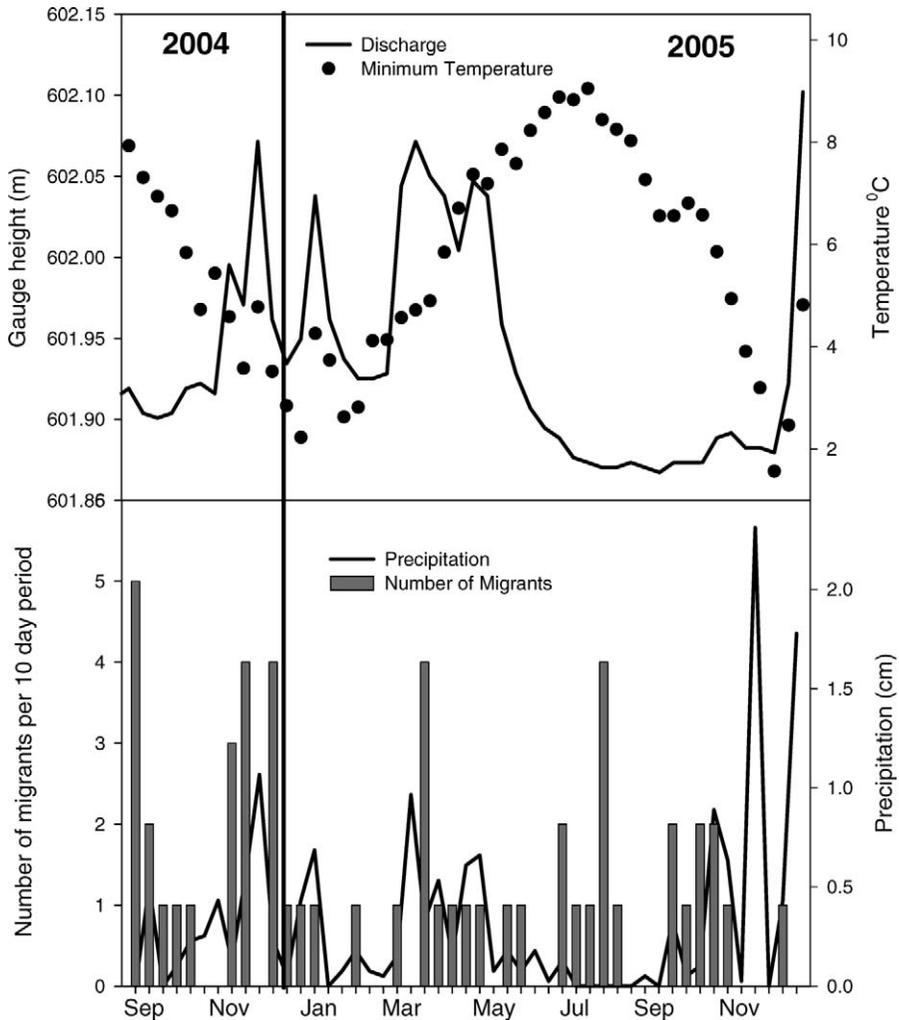


FIGURE 4.—Migration timing of juvenile and subadult bull trout (120–300 mm total length) per 10-d period (bottom panel) in relation to precipitation (cm; bottom panel), minimum temperature ($^{\circ}\text{C}$; top panel), and discharge (as represented by gauge height, m; top panel) in the South Fork Walla Walla River, northeastern Oregon, 2004–2005.

parsimonious model of migration cues included only minimum temperature (number of migrants/10-d period $= 0.42 + [0.07 \times \text{minimum temperature}] + \varepsilon$, where ε = error term; $R^2 = 0.03$; $P = 0.11$; Table 1). Given the high degree of variability in migration observed across seasons, we subsequently modeled seasonal migration in response to the environmental and biological variables that appeared in the highest-ranked annual models. Within each season, there was a clear best model (i.e., one that differed from the other models by more than two AIC points; Burnham and Anderson 2002). The highest-ranked models for winter and spring indicated that migration timing was negatively related to changes in minimum temperature (winter: R^2

$= 0.31$, $P = 0.06$; spring: $R^2 = 0.35$, $P = 0.05$; Table 1). Summer migration timing was positively related to changes in minimum temperature and negatively related to the number of adults moving upstream ($R^2 = 0.23$, $P = 0.13$; Table 1). Finally, the highest-ranked model of fall migration indicated that migration timing was positively related to changes in minimum temperature and stream discharge ($R^2 = 0.31$, $P = 0.02$; Table 1).

Discussion

Our evaluation of juvenile and subadult bull trout movement patterns and the variables providing cues for migration revealed that movement and migration occur

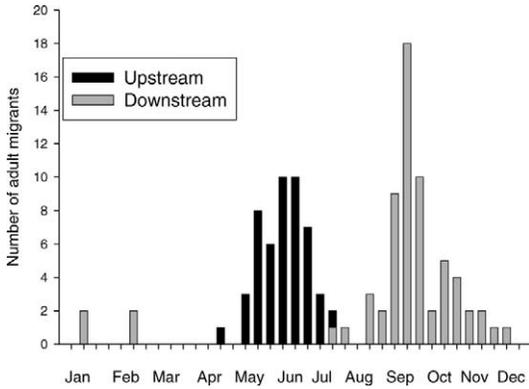


FIGURE 5.—Timing of upstream (black bars) and downstream (gray bars) migration by passive integrated transponder tagged adult bull trout (>300 mm total length) detected in the South Fork Walla Walla River, northeastern Oregon, 2003–2005.

continuously. Within our study area, we detected upstream and downstream movements throughout the year, and the longest movement from initial capture location to subsequent recapture location was 14 km. Similarly, downstream migration occurred throughout the year and almost exclusively at night. Several migratory fish were eventually detected at Nursery Bridge Dam, while others inhabited the SFWWR and Walla Walla River between the Harris Park and Nursery Bridge Dam antennae. The seasonal timing of migration was significantly and differentially associated with minimum temperature (every season), discharge (fall only), and the presence of upstream-migrating adults (summer only), but those associations explained only a portion of the variation in migration timing.

Historically, bull trout migration patterns have been described as occurring over discrete time frames (e.g., Fraley and Shepard 1989; Swanberg 1997). However, we observed a much broader temporal continuum of migration that was consistent with reports for other systems. Hemmingsen et al. (2001b) observed a similar movement pattern of fluvial juvenile bull trout in nearby Mill Creek (movement peaks occurred in spring and fall), and Downs et al. (2006) noted continuous migration of adfluvial juvenile bull trout in Idaho (spring and fall peaks). As such, it appears that the timing of juvenile and subadult migrations is more flexible and continuous than the discrete migrations of adults.

In contrast to the categorical movement distances typically used to describe bull trout life history forms (e.g., 0–2-km movements by residents; Jakober 1995), movement and migration distances within the study

population occurred on a spatial continuum. Juvenile and subadult bull trout exhibited movements of up to 14 km in the study area, and several bull trout migrated 45 km from the initial tagging location (based on detection at Nursery Bridge Dam). Bull trout movement distances within our study area were longer than those typically associated with resident fish (Jakober 1995; Chandler et al. 2001). According to our definition of migration (entailing a distinct habitat shift), movements that occurred within our study area would not constitute migration and therefore could be attributed to resident fish. If so, the greater distance moved by these resident fish relative to observations in other systems (e.g., Jakober 1995; Chandler et al. 2001) illustrates a potential movement variability that could be related to local productivity, habitat availability, or behavioral plasticity. The migration distances we observed for fish that exited the study area (up to 45 km from Reser Creek to Nursery Bridge Dam) were similar to those observed in Oregon by Hemmingsen et al. (2001a); however, we found that fish did not migrate to a common destination and that they inhabited areas of the stream that were previously considered to be migratory corridors. Regardless of our definitions for the observed behavioral patterns, the outcome is the same: throughout the year, fish are using (and moving through) the entire SFWWR, including areas once considered migratory corridors.

Migration patterns varied temporally and spatially and also differed between daytime and nighttime. As in other studies (Jakober 1995; Ratliff et al. 1996), we found that most migrations occurred at night, particularly in the hours after sunset and just before sunrise. Nighttime movements are important in allowing smaller bull trout to escape the predation risk from larger bull trout and other predators. Along with commencing migrations at night, bull trout also display a distinct diel habitat shift into shallower water, a strategy that may allow them to prey on smaller conspecifics (Muhlfeld et al. 2003). The combination of diel movements and habitat shifts reflects an evolutionary adaptation that allows bull trout to maximize foraging opportunity while minimizing mortality risk and probably contributes to increased overall fitness (Werner and Hall 1988).

Based on seasonal models, bull trout migrated differentially across seasons and in association with changes in minimum temperature, discharge, and the presence of adult upstream migrants (during select seasons). However, environmental and biological variables alone did not explain the overall variability in migration patterns. Whereas maximum stream temperature is commonly identified as a limiting factor for bull trout (Selong and McMahon 2001), we found

that minimum temperature was more closely associated with seasonal migration timing and that the association differed across season. The mechanism by which temperature influences migration probably differs across seasons. For example, anchor ice in winter may prompt downstream movement (Jakober et al. 1998), whereas declining temperatures in the fall may act as a migration cue by decreasing fish metabolism or the availability of forage (Leggett 1977) and by marking the transition between summer hyperphagia and slower rates of consumption in winter (Lagler et al. 1962).

We observed less-consistent effects of discharge and the presence of adult upstream migrants on migration timing. Rather than observing an effect of discharge on migration timing in the spring (during peak flows), we observed a positive association in the fall. However, it is possible that a relation between spring discharge and migration timing was obscured because discharge both peaks and reaches base flow during this season. The association between summer migration timing and upstream-migrating adults was anticipated, as this was the only season in which adult migrants could influence migration timing (via predation: Beauchamp and Van Tassell 2001). Ultimately, while biological and physical explanations of the effects of temperature, discharge, and the presence of adult upstream migrants as stimuli for migration are feasible, the low overall explanatory power of our models suggests that other contributing factors probably influence migration patterns.

Despite the large number of fish that were tagged across multiple years of sampling, there were two notable limitations to our study: (1) variable detection efficiency at antennae and (2) the inability to tag and monitor movements of fish smaller than 120 mm TL. The variability in detection efficiency was primarily due to a few unavoidable episodes of antenna inoperability (electrical outages at both antennae in 2003 and 2004 and a fire near the Bear Creek antenna in 2005) rather than to high variation in antenna efficiency (Zydlewski et al. 2006). Nevertheless, our data set of known migrants might have been larger if the antennae had operated 100% of the time. The Bear Creek antenna was among the first remote, solar-powered antennae to be installed via helicopter deposit of equipment into roadless wilderness. While this approach allowed us to monitor movements and obtain recaptures in an upper headwater area of a bull trout stream that has rarely been studied at this scale, we were limited by the logistics and technology available. We were forced to infer movement direction based on the known capture location and eventual detection at an antenna location; recent advances have addressed this

issue with the installation of multiple antennae at a single location.

Second, because we only tagged and monitored the movements of fish larger than 120 mm TL, our inferences about juvenile and subadult movement patterns do not apply to smaller fish. Fish that are smaller than 120 mm TL (i.e., age 0 or 1) may show alternate movement patterns in response to cues that are important for larger fish, or they may respond to cues that have no influence on movements of larger fish. For example, Hemmingsen et al. (2001a) observed a large number of bull trout (89–250 mm fork length; very few were below 120 mm) migrating downstream in late April and early May. For these fish, discharge may be a more important migration cue than temperature change. Furthermore, Mogen and Kaeding (2005) observed that juvenile bull trout commenced migrations at age 2 or 3. These studies suggest that our tagging and monitoring of larger juvenile bull trout allowed us to describe the majority of downstream movements. Nevertheless, it will still be important to also quantify small-fish movements and associated cues.

Despite these potential limitations, our work represents the first multiple-year study to use both active (mark–recapture) and passive (antenna) detection techniques and a very large number of tagged individuals to examine movement patterns of a fluvial bull trout population. This intense sampling effort allowed us to identify individuals that exhibited migratory movements, assess the timing of migration, statistically evaluate multiple environmental and biological variables that might act as cues for migration, and describe the distribution of migration distances. Rather than select large fish for a priori monitoring (e.g., telemetry study), our mark–recapture technique allowed us to acquire movement information for the whole population of fish exceeding 120 mm with little sample bias (Al-Chokhachy 2006; Al-Chokhachy et al., in press). Finally, this study employed multiple sampling and monitoring techniques that together provided a thorough and detailed description of the continuum of migratory behavior displayed within the SFWWR population.

The observed year-round temporal and spatial migration continuum of juvenile and subadult bull trout has some important management implications. While previous discussions of migration patterns have suggested that fish use migratory corridors during discrete time intervals and that they move in association with various cues in the environment, our study demonstrates that fish (1) move and migrate throughout the year, (2) can respond unpredictably to specific cues or combinations of cues when commencing migration,

and (3) utilize supposed migratory corridors as year-round habitat in some cases. In the same way that our understanding of trout migration evolved from the restricted movement paradigm (Gowan et al. 1994) to a broader understanding of variable movement patterns (Gowan and Fausch 1996; Bahr and Shrimpton 2004), our results indicate that a reevaluation of bull trout movement pattern descriptions is warranted.

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