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ARTICLE

Life Histories, Demography, and Distribution of a Fluvial Bull Trout Population

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Abstract

To describe the life histories and demography of a fluvial population of Bull Trout *Salvelinus confluentus*, we PIT-tagged and radio-tagged Bull Trout captured in Mill Creek, a tributary of the Walla Walla River (Washington–Oregon), during 1998–2009. Adult abundance declined 63% during 2006–2010, driven primarily by a 10-fold reduction in subadult-to-adult returns. Larger subadults and fall–winter emigrants survived at higher rates, but they were a small proportion of the subadult migrants. The survival rates of larger, generally older adults were also more than 40% greater than those of smaller adults. Changes in abundance influenced other characteristics of the population. For example, adult upstream movement into spawning areas during 1999–2005 peaked in late July, whereas the smaller runs observed during 2006–2010 peaked in early September, and the relationship between fish size and migration timing shifted. Unlike many adfluvial populations, more than 90% of the adults in Mill Creek spawned annually. Bull Trout that spawned in main-stem Mill Creek were primarily larger migratory adults; however, about 20% of the large adults were strictly or intermittently resident, remaining in the spawning area year-round. The downstream extent of individuals' migratory distributions varied greatly—from just downstream of the spawning area to the mouth of the Walla Walla River and potentially hundreds of kilometers into the Columbia River. Despite a large sample size of radio-tagged fish, radiotelemetry substantially underestimated the distribution and range that were evident from PIT tag detections. Life history terms such as "migratory," "resident," and "fluvial" and their associations with body size, movement, and distribution are useful for describing general patterns, but they fail to reflect the diversity and complexity within and among populations. For Bull Trout in Mill Creek, that life history diversity, including small, resident adult forms in the tributaries and a continuum of distribution for large adults, maximizes the use of available habitat and likely contributes to the population's persistence.

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Knowledge of the life history, demography, and distribution of a species is critical to its management and conservation, particularly for a potentially highly migratory species like the Bull Trout *Salvelinus confluentus*, which is classified as a species at risk in the western United States and Canada. For example, the identification of where and when Bull Trout use a river system at various stages of the life cycle, their growth and survival rates, size and age at maturation, spawning frequency, and other characteristics are key to defining a Bull Trout population, assessing the population's status, setting management objectives, identifying and remedying the limiting factors, and monitoring abundance and other population attributes (Northcote 1997; USFWS 2002). Diverse life history strategies are also important for the persistence of individual populations and the species as whole (Rieman and McIntyre 1993; Bowerman et al. 2014). Consequently, an understanding of life histories is important in maintaining that diversity.

In 1992 the U.S. Fish and Wildlife Service (USFWS) was petitioned to list the Bull Trout for protection under the Endangered Species Act due to concerns about population declines. The Bull Trout was eventually listed as a threatened species (USFWS 1999). Planning for the present study began in 1994, and at that time, most of the available information on the life histories, demography, and distribution of Bull Trout was based on a few studies of large adfluvial populations using lakes and reservoirs in Idaho, Montana, and southwestern Canada (e.g., Fraley and Shepard 1989; Pratt 1992). Little was known about the fluvial and resident forms that were presumed to dominate much of the species' remaining distribution in strictly riverine systems. Since then, substantial progress has been made in our understanding of Bull Trout biology and ecology (e.g., Brewin et al. 2001). However, a number of recently published studies on these aspects of Bull Trout biology have also focused on adfluvial populations (Downs et al. 2006; Johnston et al. 2007), and substantial gaps in information on the other life history forms remain (Al-Chokhachy and Budy 2008; Watry and Scarnecchia 2008).

The general characteristics of migratory Bull Trout have been described as follows. Spawning and juvenile rearing occur in headwater reaches. Initial emigration of "subadults" (juveniles transitioning to adults; after Northcote 1997) from natal areas typically occurs during spring through fall at ages 1–3 (Pratt 1992; Downs et al. 2006; Homel and Budy 2008). Various environmental cues (e.g., temperature and discharge) have been linked to the migration timing of subadult Bull Trout (Homel and Budy 2008). Subadults exhibit accelerated growth as they become more piscivorous (Goetz 1989; Rieman and McIntyre 1993; Beauchamp and Van Tassell 2001). Subadults typically spend several years in larger rivers (fluvial life history) or in lakes or reservoirs (adfluvial life history) and then return to natal areas to spawn as mature adults (at ages 4–7; Rieman and McIntyre 1993; Mogen and Kaeding 2005; Muhlfeld and Marotz 2005). The upstream migration of adults to spawning reaches extends from April through September (Pratt 1992; Swanberg 1997; Starcevich et al. 2012). Both consecutive-year spawning and nonconsecutive-year spawning have been reported for Bull Trout (Pratt 1985, 1992; Goetz 1989; Watry and Scarnecchia 2008). The size of migratory adults generally ranges from 290 to 880 mm, although larger individuals are occasionally observed (Goetz 1989). Resident adult Bull Trout are thought to be smaller (<300 mm) and continuously reside in the same habitat where spawning and juvenile rearing occur (Mullan et al. 1992; Pratt 1992; Nelson et al. 2002).

Given the differences in Bull Trout life history patterns, the range of life history characteristics, and the potential influences of different environments on those attributes, more specific information on Bull Trout populations in the region—particularly fluvial life history forms—was considered essential to aid in Bull Trout recovery. Our objective was to describe the movement patterns and demographics of fluvial subadult and adult Bull Trout. Specifically, we investigated migration timing, distribution, size, growth, age structure, maturity, sex ratios, subadult-to-adult return and survival rates, and adult-to-adult return and survival rates. We also assessed potential influences of water temperatures and discharge on return and survival rates and on subadult migration timing.

STUDY AREA

Mill Creek flows into the Walla Walla River, a Columbia River tributary on the border of northeastern Oregon and southeastern Washington (Figure 1). Redd surveys conducted prior to this study (U.S. Forest Service [USFS], unpublished data) indicated that Bull Trout occupying redds were commonly 300 mm or larger, which is characteristic of fluvial fish. Anecdotal observations of Bull Trout in lower Mill Creek also suggested the presence of migratory forms. Almost all of the Bull Trout spawning occurred upstream of the Mill Creek intake dam at river kilometer (rkm) 41 (Howell and Sankovich 2012). The presence of a fish ladder at this dam provided an opportunity to tag and recapture migratory Bull Trout.

The Mill Creek watershed above the intake dam encompasses 8,798 ha (James et al. 2001), and the total drainage area of Mill Creek is about 42,734 ha (USACE 2011). Water from Mill Creek is diverted at the dam and used as a municipal water supply for the City of Walla Walla, Washington. The watershed above the dam has been closed to public entry since 1974. The area is largely roadless and is also closed to grazing and timber harvest. Main-stem Mill Creek, where most of the Bull Trout spawning and juvenile rearing had been observed, extends for approximately 12.6 km above the Mill Creek intake dam (USFS, unpublished data). Average channel widths in that section ranged from 8.7 m at the lower end to 3.5 m at the upper end. Mill Creek tributaries that are situated above

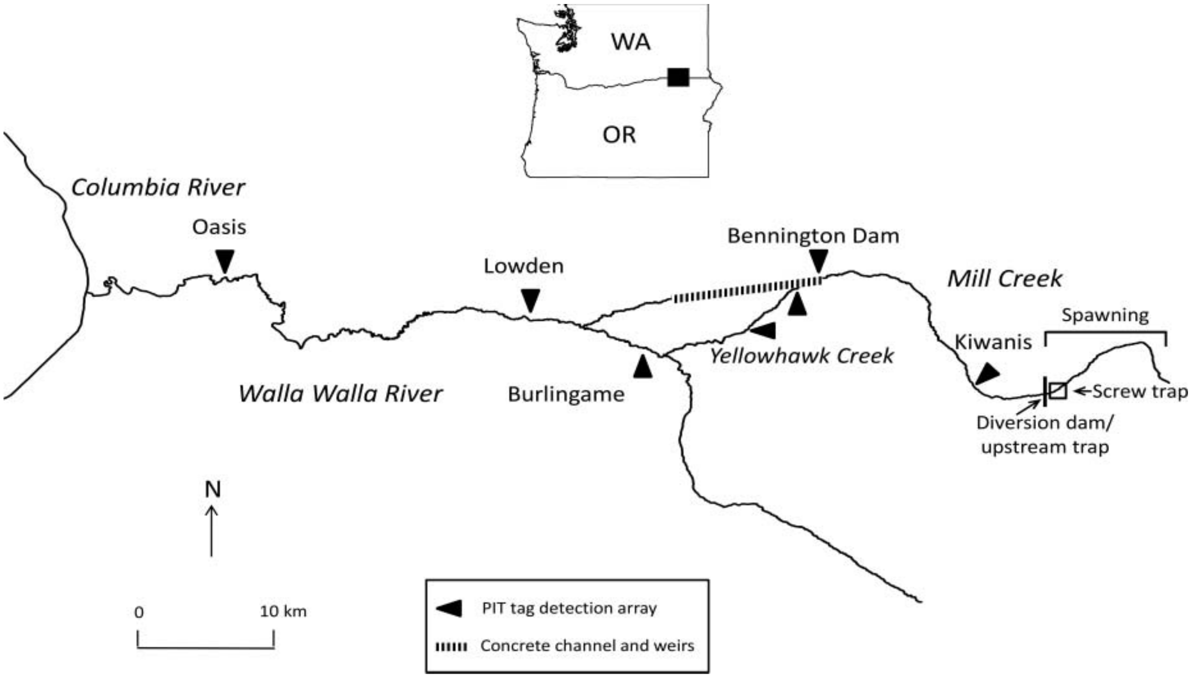

FIGURE 1. The Mill Creek study area, Washington–Oregon, including the locations of traps, PIT tag detection arrays, and the Bull Trout spawning area.

the intake dam are short (<6 km of perennial flow) and contribute small amounts of flow (≤ 0.2 m^3/s each) during summer low-flow conditions (USFS, unpublished data).

The Mill Creek watershed becomes increasingly altered by land and water usage with increasing distance downstream of the intake dam. The valley from the intake dam downstream to Bennington Dam (a flood control structure) has been used for agriculture, timber production, and rural residential development. There was no ladder for upstream fish passage at Bennington Dam until 1982 (40 years after the dam was built); however, the ladder has continued to impede passage (Koch 2014). Below Bennington Dam, Mill Creek is confined to a concrete channel for 11 km through the City of Walla Walla (Figure 1; NPCC 2004). About 1.6 km downstream of Bennington Dam, water is diverted into Yellowhawk Creek, which enters the Walla Walla River upstream from the Mill Creek mouth (Figure 1). Yellowhawk Creek provides additional connectivity with the mainstem Walla Walla River, and its habitat is less altered than that of lower Mill Creek (i.e., through the concrete channel). During the summer, the diversion of water into Yellowhawk Creek largely dewaters Mill Creek downstream. Lower Mill Creek and Yellowhawk Creek contain a number of obstructions that hinder fish passage (NPCC 2004; USACE 2011). Flow diversions for irrigation and other uses also completely dewater some reaches of the lower Walla Walla River. High water temperature is a primary concern in the Walla Walla River drainage (NPCC 2004). Portions of lower Mill Creek, Yellowhawk Creek, and the lower Walla Walla River have been listed as water quality impaired based on temperature, dissolved oxygen concentration, pH, fecal coliform level, and chemical contaminants (WDOE 2008).

Besides Bull Trout, the following fishes are found in upper Mill Creek: Rainbow Trout/steelhead *Oncorhynchus mykiss*, sculpins *Cottus* spp., Western Brook Lamprey *Lampetra richardsoni*, suckers *Catostomus* spp., and Mountain Whitefish *Prosopium williamsoni*. Adult spring Chinook Salmon *Oncorhynchus tshawytscha* from excess hatchery returns in other basins have occasionally been relocated to upper Mill Creek for spawning. Lower reaches contain Longnose Dace *Rhinichthys cataractae*, Speckled Dace *Rhinichthys osculus*, Umatilla Dace *Rhinichthys umatilla*, Leopard Dace *Rhinichthys falcatus*, Chiselmouth *Acrocheilus alutaceus*, Peamouth *Mylocheilus caurinus*, Redside Shiner *Richardsonius balteatus*, Northern Pikeminnow *Ptychocheilus oregonensis*, and several species of introduced centrarchids and ictalurids (NPCC 2004).

METHODS

We used a combination of downstream and upstream traps and PIT tags to collect data on Bull Trout movement timing, size, growth, maturity, and survival. Distribution was determined by detections at PIT antenna arrays in Mill Creek and the Walla Walla River and by radiotelemetry conducted for a subsample of the PIT-tagged individuals. Specific methods are described below.

Trapping and PIT-tagging.—Upstream-migrating Bull Trout, which were suspected to be primarily adults, were trapped as they exited the fish ladder at the intake dam prior to spawning (Figure 1). A steel cube (~1 m high, 1 m wide, and 1.5 m long; made primarily with 10-mm mesh) was bolted to the exit of the fish ladder. A hoop net (1 m in diameter and 2 m long) was attached to the upstream end of the metal cube; the net was equipped with internal fykes to prevent fish from going back down the ladder. Fish were removed from the hoop net (hereafter, "upstream trap") for sampling. The dam was 2.5 m high, and we installed a vertical net to further prevent Bull Trout from going upstream over the dam without passing through the fish ladder. In 1998 (the first year of the study), the upstream trap was operated during March–October to initially determine the full duration of the upstream migration. Based on those data, the upstream trap was operated from mid-May through mid-October during subsequent years of the study (1999–2010).

Bull Trout (primarily subadults) moving downstream were captured by using a 1.5-m-diameter rotary screw trap that was located approximately 0.5 km upstream of the intake dam (Figure 1). We operated the trap during March–October in 1998–2010; during November–February in 2001 and 2002; and during November and December in 2008 and 2009.

Bull Trout that were captured in either the upstream trap or the rotary screw trap were anesthetized with tricaine methanesulfonate (MS-222; 60 mg/L), measured for FL, weighed, and scanned for the presence of a PIT tag. Scale samples were also taken. Bull Trout without PIT tags were given tags of different sizes depending on individual fish size. In 1998–2004, 150-mm and larger Bull Trout received 11.5- and 14-mm tags. During 2005–2007, 140-mm and larger fish received 23-mm tags, and 100–139-mm fish received 11.5-mm tags. In 2008–2010, 150-mm and larger fish received 23-mm tags, and 100–149-mm fish received 11.5-mm tags. Changes in tag sizes (and frequency) reflected the changes in tag technology, size, availability, and standardization in the Columbia River basin over the course of the study. During 1998–2004, a tagging syringe was used to inject 11.5–14.0-mm tags either (1) into the abdominal cavity for fish smaller than 300 mm; or (2) into the sinus at the base of the dorsal fin for 300-mm and larger fish. Beginning in 2005, 23-mm tags were implanted in the abdominal cavity through a small incision located anterior and dorsal to the pelvic girdle in fish smaller than 300 mm; the 23-mm tags were implanted through a small, subcutaneous incision in the dorsal sinus for 300-mm and larger fish. The incisions were swabbed with isopropyl alcohol, dried with a cotton swab, and closed with a drop of veterinary-grade tissue adhesive. The fish were allowed to recover in buckets of aerated stream water before they were released. The PIT tag retention rate was 93% for Bull Trout in the South Fork Walla Walla River, where similar tagging methods were used (Al-Chokhachy and Budy 2008). During 2002–2007, fish that were captured in the upstream trap were inspected with ultrasound to determine sex and maturity status (Evans et al. 2004; Howell and Sankovich 2012).

During 1998–2002, a portion of the subadults that were captured in the screw trap also received a caudal fin mark, which allowed us to identify them for estimation of trap efficiency via the methods of Johnston et al. (2007). We alternated between the upper and lower caudal lobes weekly. After these fish recovered from anesthesia, they were released into a pool about 200 m upstream of the screw trap. Efficiency of the screw trap was determined monthly from the number of recaptured, fin-marked Bull Trout. Average monthly efficiencies during 1998–2002 were used to adjust raw screw trap catches for the analysis of subadult migration timing. Bull Trout that were not marked for estimation of trap efficiency were released downstream of the screw trap.

Detections of PIT tags.—Fish with PIT tags were recaptured in the upstream trap and the screw trap throughout the study. To help define downstream movements, we worked in coordination with the USFWS (Koch 2014) to install PIT tag detection arrays (Zydlewski et al. 2001) between February 2005 and November 2007. Antenna arrays were installed at two sites in Mill Creek, two sites in Yellowhawk Creek, and three sites in the lower Walla Walla River (Figure 1). Each antenna array was custom built for the specific site and included a full-duplex interrogation system (Destron Fearing Model FS1001A or Model FS1001M).

Since we did not have multiple arrays at each site to determine the direction of fish movement (e.g., Connolly et al. 2008), PIT tag detections were classified as downstream or upstream movements based on the sequence of detections at the arrays. For example, a subadult that was tagged at the screw trap was categorized as moving downstream if it was initially detected at the Kiwanis array and subsequently detected at the Bennington array and other arrays downstream until reaching its downstream-most location. The direction of multiple detections at the same array was based on the order of the detections occurring after the initial detection. For example, if a fish was initially detected as moving downstream at an array, and it was next detected at that same array, the second detection would be classified as an upstream movement.

To estimate detection efficiency at the arrays, we first identified all instances in which a fish passed undetected at a given array between two locations where the fish was detected. We then summed the detections at each array and calculated array efficiency (E) as

$$E = \frac{D}{(D + M)}, \tag{1}$$

where D is the number of detections, and M is the number of missed detections.

For the Oasis array near the mouth of the Walla Walla River, there was no downstream array with which to determine the number of missed detections. In this case, we used the efficiency estimated by Anglin et al. (2010), which was based on physical factors, such as flow and antenna performance (e.g., antenna read range). Efficiencies were estimated separately for upstream and downstream movements of subadults and adults because flow, tag size, fish location in the water column, tag detection distance of the array, and other factors could vary seasonally and with fish size. The total number of PIT-tagged Bull Trout passing an array (B) was then calculated as

$$B = D\left(\frac{1}{E}\right). \qquad (2)$$

To describe the farthest downstream distribution of PIT-tagged fish, we used only those detections occurring after November 2007, when the system of arrays was fully installed.

Age estimation.—Scales were impressed on cellulose acetate cards, which were magnified to permit annulus counts similar to the methods of Mogen and Kaeding (2005). Determination of age based on scales can be inaccurate for larger, older Bull Trout, as evidenced by other studies (Hanzel 1985; Mogen and Kaeding 2005; Zymonas and McMahon 2009) and by data from the present study. However, it does appear to be consistent with other methods for aging smaller, younger fish. For example, Fraley et al. (1981) found no error in scale-based ages relative to otolith-based ages for age-0–3 Bull Trout. Consequently, the reporting of scale-based ages in the present study was limited to subadults ($<$270 mm FL). Adult age composition was based on adult recaptures of PIT-tagged subadults. The first year in which a PIT-tagged subadult was recaptured as an adult ($\geq$270 mm FL) was classified as “adult age 1.”

Telemetry.—Prior to installation of the PIT antenna arrays, we used telemetry to describe Bull Trout movements and timing and to collect finer-scale distribution data. During 1997–1999, 46 adult-sized Bull Trout (FL range = 282–630 mm) were captured in the upstream trap, in the screw trap, and by angling in the pools above and below the intake dam. The fish were tagged with radio tags (Lotek Model NTC-6-2; or Advanced Telemetry Systems Model 375, 384, 386, 393, 2-357, or 2-375) and were tracked through 2002. Among the 46 radio-tagged Bull Trout, 20 individuals were tracked for one to three annual cycles of spawning, overwintering, and returning to spawn.

Between late April and early August 2006, 31 subadults (FL range = 165–250 mm) that were captured in the screw trap were radio-tagged via the same procedures used for adults. The minimum FL of radio-tagged fish was set at 164 mm to ensure that the tag weight was no more than 3% of fish body weight. Radio tags (Lotek Model NTC-3-2-KMF) with a 12-h duty cycle and a 15-s burst rate were used for subadults. The fish also received an 11.5-mm PIT tag. The tag life and tracking duration averaged 108 d (SD = 60).

Tagged adults and subadults were tracked once or twice per week from a vehicle (downstream of the intake dam) or on foot (upstream of the dam). In addition, tracking from a fixed-wing airplane was conducted from the Walla Walla River mouth upstream throughout the length of Mill Creek; this method allowed us to check for fish in locations that were inaccessible by vehicle or on foot.

Water temperature and flow.—We examined temperature and flow in relation to the downstream movement of subadults and assessed their potential influences on survival rates. Stowaway, Tidbit, and Hobo Water Temp Pro v2 temperature loggers (Onset Computer, Inc., Pocasset, Massachusetts) that were programmed with 45-min or 1-h recording intervals were placed in well-mixed zones at the screw trap and PIT tag detection arrays in Mill Creek and in the lower Walla Walla River. Additional temperature and flow data were obtained from (1) the City of Walla Walla for the Mill Creek intake dam, (2) the U.S. Geological Survey (USGS) and the Washington Department of Ecology for gauging stations, and (3) the Washington Department of Fish and Wildlife (WDFW).

Analysis of age, size, growth, and migration timing.—For statistical comparisons of two groups, we used a t-test when the data were normally distributed and when variances were equal. When those assumptions were not met, we used a Mann–Whitney rank-sum test. For comparisons of more than two groups, we used a Holm–Sidak one-way ANOVA for normally distributed data with equal variances. When the assumptions of that analysis were not met, we used a Kruskal–Wallis one-way ANOVA and Dunn’s multiple comparison test. For all tests, α was set at 0.05.

Mark–recapture analysis.—The mark–recapture analysis was complicated by the tagging and recapture of Bull Trout in subadult and adult size-classes. Due to missing values (i.e., unknown size between recaptures), it was not possible to account for the effect of size at recapture on demographic parameters by using a Cormack–Jolly–Seber model as implemented in Program MARK (Cooch and White 2006; White et al. 2006). Instead, we used a multistate model with directed growth transitions to estimate state-specific apparent survival (S) and recapture probability (p) for subadult and adult Bull Trout that were tagged in Mill Creek. Subadults were initially tagged at the screw trap and were recaptured as adults, primarily at the upstream trap. Adult recaptures included (1) subadults that were returning as adults and (2) recaptures of adults that were initially tagged at the upstream trap. Tagged Bull Trout were initially classified into six states representing differences in fish size (mm FL) at tagging and the period in which tagging occurred: (1) very small subadults ($<$147 mm) that were tagged during March–August; (2) very small subadults that were tagged during September–February; (3) small subadults (147–269 mm) that were tagged during March–August; (4) small subadults that were tagged during September–February; (5) medium adults (270–409 mm); and (6) large adults (>409 mm). The multistate model specification allowed for additional biological realism in the analysis by allowing S and p to vary among states. For this analysis, Bull Trout transitioned among size stages (i.e., growth) based on directed transition probabilities (Ψ). The multistate model was used to evaluate whether S and p varied (1) between subadults and adults over time, (2) among adult and subadult size-classes, and (3) between out-migrating subadults tagged during March–July and those tagged during August–February, as the two groups would have initially encountered different temperatures (warming versus cooling) in the migratory habitat. We also compared S between 1998–2005 and 2006–2010, when adult Bull Trout abundance substantially declined (Howell and Sankovich 2012). Additionally, annual peak flows and the number of high-flow events were evaluated for potential influences on demographic parameters. Temperature was not modeled since there was little annual variation (see Results). The multistate model was fitted via maximum likelihood in Program MARK (White and Burnham 1999) by using the RMark package for R (Laake and Rexstad 2006; R Development Core Team 2010).

Some of the model parameters were fixed at either 0 or 1 to reflect missing data or biological constraints in the multistate model. State-specific survival was set to 0 for cohorts in which no fish were tagged and released (Table 1). Since Bull Trout initially captured as subadults were never recaptured as subabults, recapture probability for that state was set to 0. The multistate model required an additional parameter, Ψ, which represents the probability of transitioning between states. Several transition parameters were fixed at 0 or 1 to reflect the biological constraints of directed growth (i.e., parameter not estimated). Specifically, Bull Trout could either remain in the same state or could transition into a larger (size) state (i.e., no reverse growth).

Seventy candidate models were developed to evaluate the analysis objectives (Table 1). Dummy variables were constructed using the design matrix in Program MARK to evaluate differences in S and p among varying size-classes, subadult out-migration timing, and heterogeneity over time. For example, to evaluate whether out-migration timing for subadults affected estimates of S, dummy variables were constructed that either fixed S to be equal (i.e., no difference in survival) among subadult states or allowed S to vary (i.e., a difference in survival) among subadult states. Candidate models were then evaluated using an information-theoretic approach (Burnham and Anderson 2002).

TABLE 1. Submodels used to estimate Bull Trout survival (S), recapture probability (p), and transition probability (Ψ) in candidate multistate models (states: a = large subadults [147–269 mm FL] tagged during March–July; b = large subadults tagged during August–February; c = medium adults [270–409 mm FL]; d = large adults [≥410 mm FL]; flow variables: Q_{peak} = peak flow; Q_{big} = number of high-flow events).

Parameter	Submodel
S	Time + $\text{State}_{a,b,c,d}$
	Time + $\text{State}_{a=b,c,d}$
	Time + $\text{State}_{a=b,c=d}$
	Time + $\text{State}_{a,b,c=d}$
	Q_{peak} + $\text{State}_{a,b,c,d}$
	Q_{big} + $\text{State}_{a,b,c,d}$
	Q_{peak} × $\text{State}_{a,b,c,d}$
	Q_{big} × $\text{State}_{a,b,c,d}$
p	Time + $\text{State}_{a,b,c,d}$
	Q_{peak} + $\text{State}_{a,b,c,d}$
	Q_{big} + $\text{State}_{a,b,c,d}$
	Q_{peak} × $\text{State}_{a,b,c,d}$
	Q_{big} × $\text{State}_{a,b,c,d}$
Ψ	$\text{State}_{a,b,c,d}$
	Time + $\text{State}_{a,b,c,d}$

Model fitting, selection, and inference.—The global model (least parsimonious, allowing unique values of S and p for each state by time) from the candidate model set was fitted to the data, and a parametric bootstrap was used to estimate a goodness-of-fit measure, $\hat{c}$ (Cooch and White 2006). This measure approaches 1.0 when the model fits the data perfectly; it is calculated as $\hat{c} = (-2 \cdot \log_e L)/df$, where L is the likelihood of the model and df is the number of multinomial cells minus the number of parameters estimated (Senar and Conroy 2004; Cooch and White 2006). The sparse nature of this data set (i.e., not all of the possible capture histories were present) limits the direct calculation and use of likelihood approaches to estimate goodness-of-fit statistics such as $\hat{c}$. Therefore, a parametric bootstrap procedure was used to estimate c by generating 1,000 replicate data sets in R from the fitted model and then fitting the global model to each bootstrap replicate in Program MARK by using RMark (Cooch and White 2006; Laake and Rexstad 2006; R Development Core Team 2010). Specifically, c was estimated as $\hat{c} = \hat{c}_{sample}/\hat{c}_{bootstrap}$, where $\hat{c}_{sample}$ is the estimated c for the observed data given the global model and $\hat{c}_{bootstrap}$ is the mean $\hat{c}$ for the 1,000 replicate bootstrap samples. We then calculated the quasi-likelihood-adjusted Akaike's information criterion corrected for small sample sizes (QAIC_c) for each candidate model by using the maximized log likelihood, the number of model parameters, and $\hat{c}$ (Burnham and Anderson 2002). This approach accounted for any lack of fit (i.e., due to extra binomial variation) in the model selection process (Cooch and White 2006). We were confident that a lack of fit was due to extra variation and not to model misspecification, as our extensive simulation study of the underlying model indicated that the expected frequencies were reasonable for the capture histories observed (M. E. Colvin, unpublished data). Additionally, $\hat{c}_{sample}$ was compared to the 1,000 bootstrap replicates to evaluate whether the observed value was more extreme than the simulated value, indicating a lack of fit.

The QAIC$_c$ difference (ΔQAIC$_c$) for each model was calculated as the difference between the model's QAIC$_c$ and the minimum observed value of QAIC$_c$. Model-specific likelihood was calculated as $e^{-0.5 \cdot \Delta \mathrm{QAIC}c}$, and relative weights ($w_{model}$) summing to 1.0 were applied (Burnham and Anderson 2002). A subset of candidate models was retained as the confidence model set, which included models that had weights within 0.9 of the cumulative w_{model}. Individual weights for models that were retained in the confidence model set were then rescaled to sum to 1.0, and these values were used to calculate model-weighted parameter and variance estimates to account for model selection uncertainty (Burnham and Anderson 2002). To evaluate differences between 1998–2005 and 2006–2010, the state-specific mean survival was calculated for each period by using model-weighted estimates of S.

Return rates.—The return rates (RRs) for PIT-tagged subadults and adults were calculated for the same classes (i.e., based on fish size and emigration timing) used in the mark–recapture analysis. For subadults, these were subadult-to-initial-adult RRs (i.e., adult recruitment), since 99% of the recaptures in the years after tagging were 270-mm and larger fish (see below). The RRs did not include the annual survival of subadults that survived for one or more years but did not eventually return as adults. Although the RRs underestimated true survival (because they did not explicitly account for detection probability or p), we consistently captured about 80% of the adult population in our upstream trap (Howell and Sankovich 2012), and an additional 8% of the adults were recaptured in the screw trap (see Results), indicating a high overall efficiency of our traps in recapturing tagged adults. We also adjusted our annual RRs to account for marked fish that were not recaptured in a given year but that were alive and recaptured in a later year,

$$\mathrm{RR} = \frac{Y + U_{\leq x}}{N + U_{<x}}, \tag{3}$$

where RR is the return rate in year $x + 1$; Y is the number of marked fish that were recaptured in year $x + 1$; $U_{\leq x}$ is the number of fish marked in year $\leq x$ that were not recaptured in year $x + 1$ but were recaptured in a later year (year $x + 2$, $x + 3$, etc.,); N is the number of marked fish that were initially tagged or recaptured in year x; and $U_{<x}$ is the number of fish marked in year $<x$ that were not recaptured in year $x + 1$ but were recaptured in a later year (year $x + 2$, $x + 3$, etc.).

To estimate the adult population size for comparison to survival rates and RRs, we followed the methods of Howell and Sankovich (2012). We used annual upstream trap counts of adults (≥270 mm FL) and a mark–resight estimate to account for fluvial adults that overwintered upstream of the trap.

RESULTS

Classification of Subadults and Adults

Bull Trout smaller than 270 mm were classified as subadults, and 270-mm and larger individuals were classified as adults. This was primarily based on the sizes of females that were identified as mature during ultrasound examination at the upstream trap (see below). Classifying the maturity of Bull Trout males based on size is more problematic since there is a wide size range of mature males, including small (100–150-mm) precocious males (James and Sexauer 1997). We were unable to definitively determine the maturity status of males at the upstream trap by using ultrasound; however, among the males that produced milt when captured at the trap, only one was smaller than 270 mm (FL = 266 mm). In any case, during 1998–2010, only 2% of all Bull Trout captured at the upstream trap (N = 1,618) were smaller than 270 mm, and only one fish that was tagged as a subadult when captured in the screw trap was recaptured in the upstream trap at a size less than 270 mm (FL = 261 mm). Likewise, only 3% of the screw-trap-captured fish were 200–269 mm; most of the 270–299-mm fish (which accounted for <1% of the total) were caught between mid-September and mid-October, and they appeared to be post-spawn adults (e.g., evidenced by abrasion of the lower caudal fin). Consequently, given the small proportion of sampled Bull Trout that were 200–299 mm, any errors in classifying individuals within that size range as subadults or adults would have little effect on the results that follow. Hereafter, we use the term "migratory" for fish that moved downstream of the spawning area (i.e., downstream of the intake dam and the upstream trap), and we use the term "resident" in reference to fish that remained in the spawning area (i.e., upstream of the intake dam) throughout the year.

Subadults

The highest screw trap catch of subadult Bull Trout typically occurred from mid-April through June (Figure 2). This period accounted for 67% of the annual catch and generally corresponded with declining spring flows and increasing temperatures. However, there did not appear to be any specific flow or temperature cues that coincided with spikes in subadult movement. For example, in both 2006 and 2007, large numbers of fish were captured (1) during mid-May to late June, when temperatures had increased to 8–10°C; and (2) at the tail of the spring runoff period, when base flow level was reached (2007) or shortly before base flow was reached (2006). However, the peak catch in 2006 occurred during the first 2 weeks of August, whereas very few fish were caught during that same period in 2007. Summer base flow rates (0.93 m^3/s in 2006; 0.94 m^3/s in 2007) and peak water temperatures (10.4°C in 2006; 10.8°C in 2007) were similar between those 2 years.

Screw trap efficiency averaged 47% (SD = 10) during March–August and 28% (SD = 17) during September–

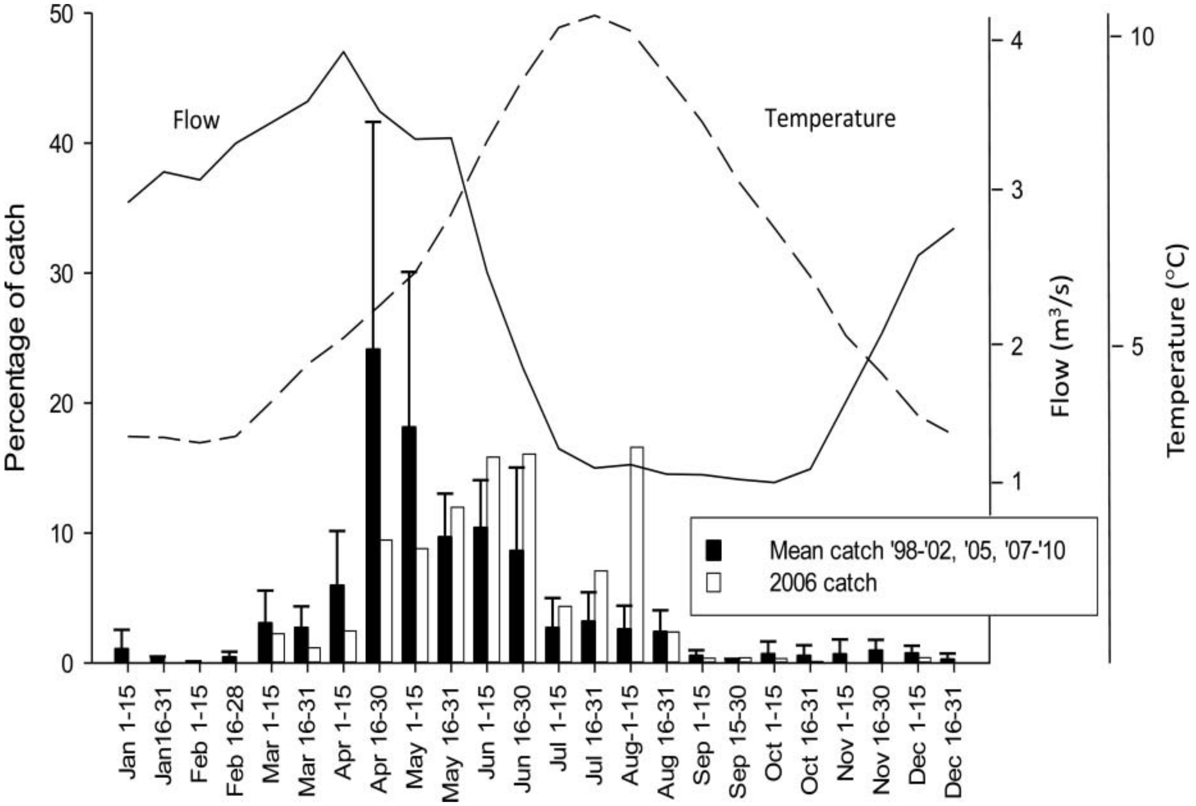

FIGURE 2. Bimonthly percentages (+SD) of the annual catch of subadult Bull Trout ($N = 7{,}652$) at the rotary screw trap in Mill Creek (1998–2010); and the mean bimonthly streamflow and water temperature at the Mill Creek intake dam (City of Walla Walla; 2001–2008). Catch was weighted for trap efficiency.

February. Efficiency was also fairly consistent during spring through early summer (range = 41–54%), when most of the catch was obtained.

Bull Trout subadults can migrate at various ages, and individuals in that size range (<270 mm FL) could also be juveniles (i.e., would continue to rear in upper Mill Creek) or small adult resident forms (i.e., would only move locally). Therefore, we did not know how many of the screw-trap-captured Bull Trout smaller than 270 mm were downstream migrants. Only 2.8% of the tagged fish were subsequently recaptured in the screw trap at a size smaller than 270 mm, and 85% of those fish were recaptured within 30 d of tagging. Only one subadult was recaptured in the screw trap at a size less than 270 mm more than 1 year after tagging. Since the screw trap was located at the lower end of the spawning and juvenile rearing distribution, this result suggests that most of the screw-trap-captured Bull Trout smaller than 270 mm were subadults that continued to move downstream. This movement pattern was generally corroborated by the telemetry data: 15 of the 16 subadults that were radio-tagged during late spring moved downstream of the Mill Creek intake dam within 1–4 weeks after tagging. The other subadult migrated in November after being radio-tagged in June.

The mean FL of captured subadults generally increased slightly from early spring through winter. Subadults that were captured during August–January were significantly larger than those captured during February–May (Mann–Whitney rank-sum test: $P \leq 0.001$); however, the differences were not large (median = 156 and 143 mm FL, respectively). Individuals that were 126–175 mm comprised 78% of the catch; 201–269-mm fish made up 3% of the catch. Ages of subadult-sized fish were estimated at 1–4 years (Figure 3). Fish in the 80–120-mm range were largely age 1. We captured very few fish that were likely young of the year (<80 mm FL; 0.002%). The FLs of age-1 and age-2 fish were significantly different from each other and from the FLs of age-3 and age-4 fish, for which the greatest overlap in FL occurred (Kruskal–Wallis ANOVA, Dunn's multiple comparison test: $P \leq 0.05$). Given the size frequency of the trap catch, most of the subadult migrants were ages 2–3.

The farthest downstream distribution of radio-tagged subadults extended from about 2 km below the Mill Creek intake dam to Bennington Dam (~21 km from the intake dam). In most cases (87%), the radio-tagged subadults reached these locations during the spring and summer shortly after tagging and remained there.

Similar to radio-tagged fish, most of the PIT-tagged subadults appeared to remain upstream of Bennington Dam (Table 2); however; 25% of the PIT-tagged individuals were detected farther downstream. Subadults were detected at all

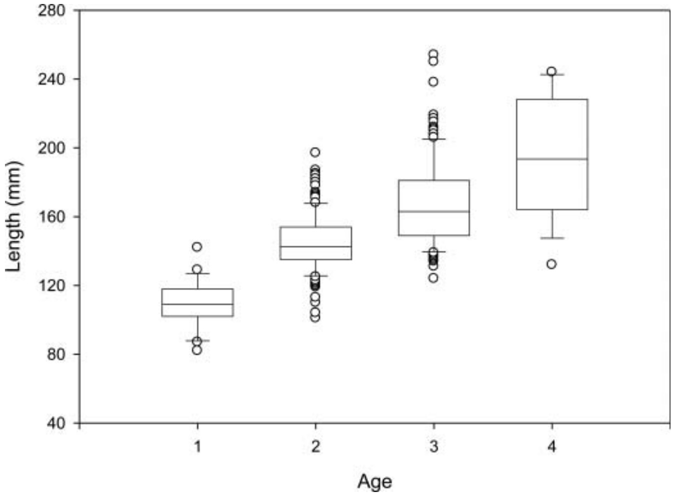

FIGURE 3. Box-and-whisker plot of FL (mm) for age-1–4 subadult Bull Trout in Mill Creek ($N = 323$ fish; line within each box = median; lower and upper boundaries of box = 25th and 75th percentiles; ends of whiskers = 10th and 90th percentiles; open circles = outliers).

sites in the lower Walla Walla River, although the numbers of detections were low. The downstream movement of subadults past the Mill Creek and Yellowhawk Creek arrays occurred primarily during spring–summer, with a slight lag in detections at successive arrays downstream (Figure 4). The detections of subadults in the lower Walla Walla River (Burlingame and Oasis arrays) indicated predominantly (93%) downstream movements during late fall and winter.

Subadult-to-Adult Transition

For most (93%) subadults, the first recapture as an adult (≥270 mm FL) in the upstream trap took place 1–2 years after tagging (Table 3). The mean FL of adults that were initially recaptured (i.e., adult age 1) 2 years after subadult emigration was greater than the mean FL of adults that were initially recaptured 1 year after subadult emigration; however, the difference was not significant (recapture year 1 versus recapture year 2, *t*-test: $P = 0.10$). Adults that were first recaptured in year 1 after subadult emigration were larger when tagged as subadults (Mann–Whitney rank-sum test: $P < 0.05$) and subsequently grew more rapidly (Mann–Whitney rank-sum test: $P < 0.001$) than adults that were initially recaptured in year 2.

Adults

The winter distribution of radio-tagged adult Bull Trout extended from the lower end of the spawning distribution near the Mill Creek intake dam downstream to near Bennington Dam, consistent with the downstream distribution of radio-tagged subadults. However, like the PIT-tagged subadults, data from the larger sample of PIT-tagged adults indicated that 35% of those adults wintered below Bennington Dam (Figure 4). Year-to-year fidelity of radio-tagged fish to wintering locations was high. More than 93% of the radio-tagged adults returned to within 0.3 km of the winter locations they occupied in previous years. The PIT tag detections (Figure 4) and the radiotelemetry data indicated that postspawn adults reached their winter locations during late October through December.

Adults that overwintered in lower Mill Creek and Yellowhawk Creek primarily began moving upstream past Bennington Dam during mid-March, with the peak movement occurring in early June (Figure 4). Peak movement past the Kiwanis array occurred about 2 weeks later.

Upstream-migrating adults were captured in the upstream trap primarily from mid-May through mid-October. Run timing during 1999–2005 was bimodal: the primary peak was

TABLE 2. Farthest downstream detection of individual PIT-tagged Bull Trout at PIT antenna arrays in Mill Creek, Yellowhawk Creek, and the lower Walla Walla River, 2007–2011 (rkm = river kilometers as measured from the mouth of the Walla Walla River; see Figure 1).

	Array					
Variable	Kiwanis (rkm 93)	Bennington (rkm 76)	Yellowhawk (rkm 70, 74)[a]	Burlingame (rkm 61)	Lowden (rkm 51)	Oasis (rkm 10)
		Subadults				
Detections	691	141	49	13	1	3
Array efficiency	0.97	0.88	0.96	0.93	0.17	0.79
Adjusted detections	712	160	51	14	6	4
Percentage of total adjusted detections	75	17	5	1	1	<1
		Adults				
Detections	60	27	8	0	0	0
Array efficiency	0.87	0.94	0.90			
Adjusted detections	69	29	9			
Percentage of total adjusted detections	65	27	8			

[a] Data from the two Yellowhawk Creek arrays were combined.

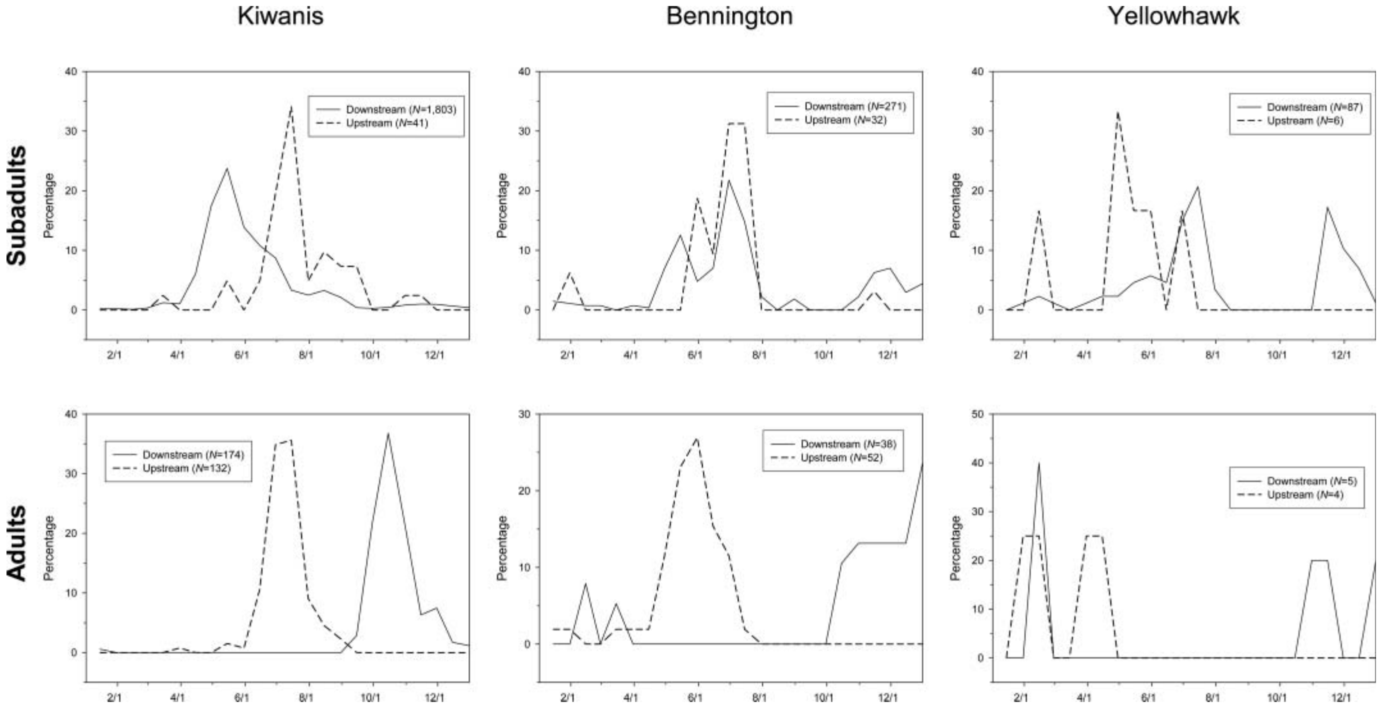

FIGURE 4. Timing (date) of downstream and upstream detections at the PIT antenna arrays in Mill Creek (Kiwanis and Bennington) and Yellowhawk Creek (two arrays combined) for subadult and adult Bull Trout that were PIT-tagged in upper Mill Creek, 2006–2011.

observed in mid-July, and the secondary peak occurred in late August through early September (Figure 5). The median run timing in 2006–2010 (i.e., when adult abundance declined) was 22 d later than that in previous years (Mann–Whitney rank-sum test: $P < 0.001$), and the peak was in early September. During 1999–2005, larger adults (>409 mm FL) were trapped earlier than smaller adults (≤409 mm FL; median date of capture = July 24 and August 9, respectively; Mann–Whitney rank-sum test: $P < 0.001$). However, during 2006–2010, after the overall shift to later run timing, there was less of a difference in run timing between the two adult size-groups (median = August 18 and August 27, respectively; Mann–Whitney rank-sum test: $P = 0.06$). Year-to-year differences in capture timing for individual adults at the upstream trap were also greater in 2006–2010 (median = 24 d) than in 1999–2005 (median = 15 d; Mann–Whitney rank-sum test: $P < 0.001$).

About 75% of the total adult recaptures of tagged subadults were first- and second-year adults (i.e., adult ages 1 and 2; Table 4). Tagged adults returned for up to 8 years. Bull Trout of adult ages 1–2 were significantly smaller than fish of adult ages 3–7 (Mann–Whitney rank-sum test: $P < 0.001$), and the FLs of adult ages 1–3 were significantly different from each other (ANOVA, Holm–Sidak multiple comparison test: $P < 0.001$; Figure 6). The median FL of all adults captured at the upstream trap was 409 mm (mean = 429 mm, SD = 90; maximum = 737 mm; N = 1,622). Adult growth rates decreased with age based on returns of tagged subadults with known adult ages (Figure 7); however, among all trapped adults, the highest growth rates were observed for intermediate-sized

TABLE 3. Year of first recapture as an adult for Bull Trout tagged as subadults, mean FL (mm) of subadults at tagging, and mean FL of subadults at first adult recapture, and mean growth per month (mm) during 1998–2009 (adult recapture year 0 = the year of tagging; year 1 = first year after tagging; etc.).

	First recapture year as an adult after tagging				
Variable	0	1	2	3	4
Number of fish	1	59	28	4	1
Percentage of fish	1	63	30	4	1
Mean (SD) FL of subadults at tagging	165	179 (27)	168 (22)	158 (16)	147
Mean (SD) FL at first adult recapture	290	357 (47)	374 (45)	427 (64)	457
Mean (SD) growth per month	35	12 (4)	8 (2)	7 (1)	7

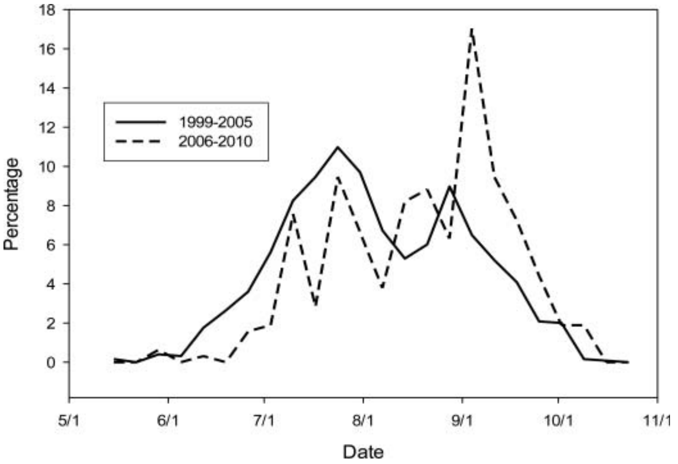

FIGURE 5. Percentage of adult Bull Trout that were captured at the upstream trap in Mill Creek on each date during 1999–2005 ($N = 1{,}248$ fish) and 2006–2010 ($N = 317$ fish).

(359–409-mm FL) fish (Figure 8). Lengths and weights were highly correlated for both subadult and adult Bull Trout (subadults: weight $= 0.000005 \cdot \mathrm{FL}^{3.14}$, $r^2 = 0.97$, $N = 2{,}637$, $P \leq 0.001$; adults: weight $= 0.000012 \cdot \mathrm{FL}^{2.97}$, $r^2 = 0.98$, $N = 1{,}727$). Growth rates measured in terms of FL and weight were generally similar before and after the decline in abundance (1999–2005: median growth = 3.5 mm/month [$N = 503$]; 2006–2010: median growth = 3.2 mm/month [$N = 74$]; Mann–Whitney rank-sum test, $P = 0.31$).

During 2002–2007 the mean FL of females identified as mature by using ultrasound at the upstream trap (430 mm, SD = 38; $N = 408$) was similar to the mean FL for the total population. Only five mature females were smaller than 300 mm FL, and they were all at least 289 mm. Migratory females were first mature on their initial return 1–4 years after being tagged as subadults. Mature females accounted for, on average, 50.7% (SD = 0.02) of the adults captured at the upstream trap during 2002–2007.

TABLE 4. Adult age composition (percentage) for all adult returns of subadult Bull Trout that were PIT-tagged in Mill Creek during 1998–2002 ($N = 120$; adult age 1 = first year of recapture as an adult; adult age 2 = recapture in the year after adult age 1; etc.).

Adult age	Percentage
1	58
2	17
3	13
4	7
5	3
6	2
7	1

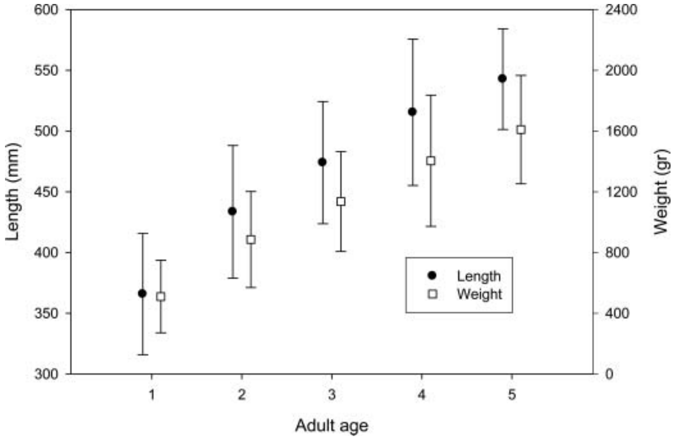

FIGURE 6. Fork length (mm) and weight (g; mean ± SD) of Bull Trout that were recaptured at adult ages 1–5 ($N = 141$ fish) after being PIT tagged as subadults in Mill Creek. Adult age 1 is defined as the first year in which a subadult was recaptured as an adult.

Ninety percent of the recaptures of tagged migratory adults at the upstream trap occurred in the year after their previous capture (Table 5). Similarly, among the mature females (i.e., ovaries with fully developing ova, 2.7–4.9 mm) that were initially captured and tagged at the upstream trap during 2002–2007, 93% were subsequently recaptured and found to be mature annually. No adult females were immature (i.e., lacking fully developing ova) when recaptured. Some of the Bull Trout that were not recaptured in successive years may have been mature and spawned during those years, since not all adults migrated below the upstream trap after the spawning

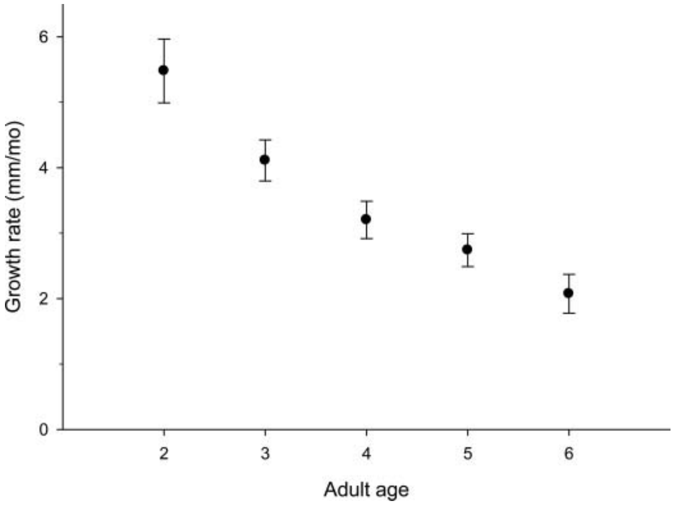

FIGURE 7. Mean (±SE) growth rates (mm/month) of adult Bull Trout that were recaptured after being PIT tagged as subadults in Mill Creek. Growth was calculated from the preceding adult year; for example, growth at adult age 2 was calculated based on the difference between the FL at adult age 1 (the first year in which the subadult was recaptured as an adult) and the FL at adult age 2 (total $N = 46$ fish; one-way ANOVA: $P < 0.001$).

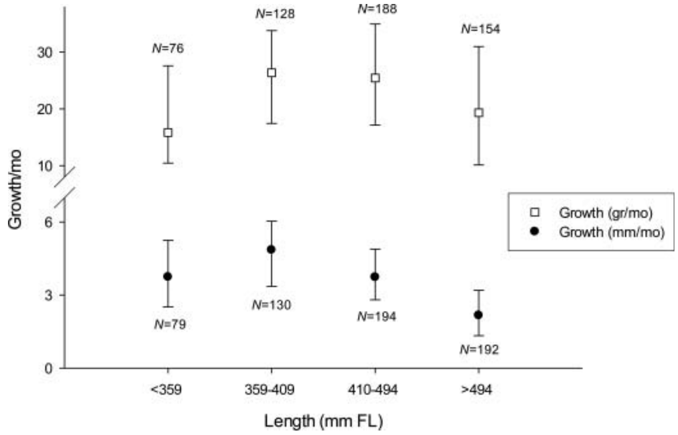

FIGURE 8. Median (with 25th and 75th percentiles) growth rates (mm FL/month and g/month) calculated from the preceding year for all adult Bull Trout that were captured at the upstream trap in Mill Creek, presented in relation to quartile FLs (total $N = 592$; Kruskal–Wallis one-way ANOVA on ranks: $P < 0.001$ for FL growth and weight growth).

period, as evident from recaptures that only occurred at the screw trap in a given year (see below). This suggests a very low rate of non-consecutive-year maturity and spawning.

Most adults were tagged and recaptured at the upstream trap (92% of the 1,693 captures and recaptures) and thus were likely migratory (i.e., moved upstream of the trap and into the spawning area during May–September and then moved downstream of the trap after spawning). Based on the PIT tag, telemetry, and trap data, subadults generally matured downstream of the trap, returned as adults to spawn upstream of the trap, and then migrated back downstream to overwinter. The remaining 8% of the adult captures and recaptures occurred exclusively at the screw trap, indicating that some adults remained in the spawning area throughout the year. Some of those adults showed strictly resident patterns (were only captured in the screw trap), including one adult that appeared to be resident over a 7-year period. The apparently resident fish were comparable in FL (271–601 mm) to the migratory adults. Most of the tagged adults that remained in the spawning area for at least 1 year exhibited mixed migratory–resident patterns. The subadults in the mixed migratory–resident group consistently remained in the spawning area until their initial recapture as adults (369–396 mm FL) and then consistently overwintered downstream of the upstream trap. Most of the fish that were tagged as adults in this mixed group were initially migratory (i.e., they were first tagged at the upstream trap) and then were resident (remaining in the spawning area) for 1–2 years, after which some resumed a migratory pattern. Adults that followed this pattern without being recaptured as residents could have been classified as migratory, non-consecutive-year spawners, thereby inflating that apparent proportion of the population.

Water Temperature and Flow

Water temperatures (7-d-average daily maximum [7DADM]) at the Kiwanis array upstream of Bennington Dam (i.e., the downstream distributional limit for most of the subadults and adults in Mill Creek) consistently remained below 16°C (Table 6). The upper thermal limit that is considered tolerable for Bull Trout is 16°C (Poole and Berman 2001), which is also the recommended water quality criterion for migratory Bull Trout habitat (USEPA 2003). However, below Bennington Dam and in the lower Walla Walla River, 7DADM temperatures reached 23.6–27.5°C, exceeded 16°C for 4–5 months, and exceeded 20°C for 2–3 months. The ultimate upper incipient lethal temperatures reported for juvenile Bull Trout are 21.0°C for a 60-d exposure and 23.6°C for a 7-d exposure (Selong et al. 2001). Although the timing of adult upstream (prespawning) movement from areas downstream of Bennington Dam indicated that most of them were not exposed to such high temperatures (Figure 4), this was not generally not the case for subadults in downstream reaches. Most of the subadult downstream migration below Bennington Dam occurred prior to and during the period of high temperatures. Although some subadults also moved upstream past Bennington Dam and the Kiwanis array to cooler reaches during summer, they represented a small percentage (2–8%) of the subadults that migrated downstream.

Summer water temperatures and flows varied little among years during the study (Table 7). Likewise, the number of

TABLE 5. Percentages of Bull Trout adults (1998–2010) and adult females (2002–2007) exhibiting various recapture intervals at the upstream trap in Mill Creek. Females were identified as mature if they had fully developing ova; females that lacked fully developing ova were deemed immature.

				Recapture interval					
Capture group	Maturity	Number of fish	Total recaptures	Succeeding year	Skip 1 year	Skip 2 years	Skip 3 years	Skip 4 years	Skip 5 years
All adults	Unknown	324	651	90	8	1	<1	<1	<1
Females	Mature	77	139	93	6	<0.1	0	0	
	Immature, previously mature	0							

TABLE 6. Average maximum 7-d-average daily maximum (7DADM) temperatures (°C) and duration of 7DADM temperatures greater than 16°C and 20°C at locations in Mill Creek and the lower Walla Walla River, 2005–2009 (rkm = river kilometer).

Location	Maximum 7DADM	Days >16°C	First date >16°C	Last date >16°C	Days >20°C	First date >20°C	Last date >20°C
Screw trap, Mill Creek intake dam	12.7	0			0		
Kiwanis array	16.0	0			0		
Bennington Dam	23.6	118	Jun 11	Sep 27	63	Jun 26	Aug 27
Yellowhawk Creek arrays[a]	26.0	126	May 26	Sep 27	85	Jun 24	Sep 16
Walla Walla River (rkm 63.7)							
Above Yellowhawk Creek[b]	24.3	116	May 26	Sep 19	73	Jun 20	Aug 31
Mill Creek mouth[b]	23.9	136	May 9	Sep 22	67	Jun 21	Aug 26
Burlingame array[a] to Beet Road[b]	23.9	106	Jun 10	Sep 19	65	Jun 26	Aug 30
Lowden array[a] to Detour Road[b]	24.6	121	May 26	Sep 24	73	Jun 23	Sep 3
Oasis array[a]	27.5	139	May 15	Oct 1	92	Jun 16	Sep 15

[a] Courtney Newlon, USFWS, unpublished data.

[b] Washington Department of Ecology (fortress.wa.gov/ecy/wrx/wrx/flows/regions/state.asp).

high-flow events was similar for the earlier period (1998–2004) and the later period (2005–2009), and there was no marked change in peak flow intensity during the two periods. Higher peak flows that could have influenced juvenile survival were observed in 2002–2004, but subadult-to-adult survival and adult survival remained relatively high through 2005 (see below).

Survival and Return Rates

Estimated $\hat{c}$ for the global model was 1.03, indicating that the global model fit the data well; the bootstrap goodness-of-fit test indicated that the model fit the data adequately ($P = 0.46$). Two candidate models were retained in the confidence model set, and they differed by how subadult S was estimated (Table 8). The models in the confidence model set predicted S as an additive function of varying state effects and time. Similarly, p was estimated by an additive model of state and time. Among the 1,972 very small (<147 mm FL) subadults that were initially tagged, only 7 fish were recaptured; very small subadults were therefore excluded from the analysis due to sparse recapture frequencies. The addition of peak flows and high-flow events as covariates influencing S and p did not improve the models.

Models in the confidence model set included the same additive recapture probability model (Table 8). This recapture probability model allowed heterogeneous state-specific p that varied over time. Model-weighted estimates of adult p were high, especially for large adults (Figure 9). Recapture probabilities declined after 2005. The confidence model set included a model with the assumption that directed Ψ among states did not vary over time. Subadult Bull Trout largely transitioned to the next adult size-class (270 mm < FL < 401 mm); medium-sized adults were equally likely to remain in the medium size-class or move into the large size-class.

The number of adults largely remained stable through 2005 and then substantially declined through 2010 (Figure 10). The corresponding RR and S for adults were relatively high in 1999–2005 (0.50 and 0.55, respectively) and then declined in 2006–2010 (0.25 and 0.34, respectively; Table 9). The RR and survival rate for subadults declined to a substantially greater extent between those periods. For large subadults, the annual RR and survival rate were 0.11 and 0.11, respectively, during 1999–2003 and then declined to 0.01 and 0.05 during 2006–2010.

Differences were also apparent between subadult migration periods and between size-classes of subadults and adults. Subadults that were captured during late summer through winter (August–February) had a higher RR and higher survival rate than subadults that were captured during spring through mid-summer (March–July; Table 9). The best-approximating model allowed Bull Trout subadult survival to vary between subadults tagged during March–July and those tagged in August–February. This model was 3.93 times more likely than the next-best-approximating model, which constrained subadult survival to be equal between the two migration timing groups. However, few subadults were captured during the August–February period. The RRs of larger subadults tagged in 2005–2009—when there was no bias in the selection of fish sizes for tagging—were more than three times higher than RRs for smaller subadults (Table 9).

Candidate models of adult survival that were retained in the confidence model set were the same. Both models allowed for heterogeneous survival rates over time. Large adult Bull Trout had the highest RRs and survival rates, which were 41–94% greater than those of medium-sized adults (Table 9; Figure 10). Even when large adults were further divided into the upper two size-quartiles (410–497 and >497 mm FL), the RRs of the two quartiles for 1999–2010 were the same (0.50). Relatively low survival was estimated for 2009–2010;

TABLE 7. July–August mean (SD) temperatures (°C) and discharge (m^3/s) in Mill Creek (1998–2009), as measured at the Mill Creek intake dam (river kilometer [rkm] 41; City of Walla Walla), the Five Mile Bridge (rkm 20.6; Washington Department of Fish and Wildlife, unpublished data), and U.S. Geological Survey (USGS) gauging station 14013000 (rkm 34.1). Peak flows and the number of high-flow events at the USGS gauging station are also shown.

			July–August mean discharge (m^3/s)		July–August mean temperature (°C)	
Year	Events > 14 m^3/s	Peak discharge (m^3/s)	Intake dam	Gauging station	Intake dam	Five Mile Bridge
1998	1	18.2		1.0 (0.1)		
1999	4	22.1		0.9 (0.1)		
2000	1	14.4		1.0 (0.1)		
2001	2	12.1		1.0 (0.2)		18.1 (0.6)
2002	2	30.6	1.1 (0.2)	0.8 (0.1)	9.6 (0.9)	
2003	1	41.9	0.8 (0.1)	0.9 (0.1)	9.8 (0.7)	18.8 (0.5)
2004	1	38.8	1.0 (0.2)	0.9 (0.2)	9.5 (0.9)	18.8 (0.6)
2005	3	16.5	0.8 (0.0)	0.9 (0.0)	8.6 (0.6)	18.3 (0.5)
2006	1	18.9	1.0 (0.1)	0.8 (0.1)	9.6 (0.8)	19.1 (0.7)
2007	1	15.1	1.0 (0.1)	0.7 (0.0)	9.9 (1.1)	18.9 (0.7)
2008	2	14.7	1.3 (0.3)	0.9 (0.2)	9.3 (0.4)	17.7 (0.5)
2009	2	45.0	1.3 (0.1)	0.9 (0.1)	9.4 (0.6)	18.1 (0.7)
Mean for 1998–2004	1.7		1.0 (0.2)	0.9 (0.1)	9.6 (0.9)	18.4 (0.7)
Mean for 2005–2009	1.8		1.1 (0.2)	0.8 (0.1)	9.4 (0.8)	18.3 (0.6)

however, there was substantial uncertainty in these estimates because those years constituted the end of the study period, when alive but undetected fish could not be determined.

Despite poorer habitat conditions below Bennington Dam, adult RRs for subadults that migrated to downstream reaches were higher in some years than the RRs for subadults that matured in the reach between Bennington Dam and the Kiwanis array (Table 10). However, subadult abundance below Bennington Dam during those years was low, as was the number of subadult-to-adult returns. Consequently, a difference of one or two returning adults could substantially affect the RRs. Return rates for adults that overwintered below Bennington Dam were also generally higher (Table 11).

DISCUSSION

In Bull Trout populations, life history forms have been classified as migratory or resident based on general migration patterns and relative body size (Rieman and McIntyre 1993). Our study indicated that although life history terminology is useful for describing broad patterns, it fails to capture the diversity and complexity within and among Bull Trout populations. Most of the Bull Trout found in main-stem Mill Creek could be described as a migratory "fluvial" form, which migrated as subadults to downstream reaches of Mill Creek and the Walla Walla River, returned to spawn in upper Mill Creek, and then migrated back downstream to overwinter in those same lower reaches. However, the migration distances of fish in the population were highly variable, extending from just below the downstream end of the spawning area to at least the mouth of the Walla Walla River and possibly hundreds of kilometers into the Columbia River (discussed below). Some adults were intermittently migratory—migrating in some years but not in others. A few fish were "resident," consistently remaining in the spawning reaches despite being indistinguishable from the migratory forms in size. Both resident and migratory forms of larger-sized Bull Trout were also observed in the South Fork Walla Walla River (Al-Chokhachy and Budy 2008). Similar behavior has been observed for Bull Trout in the Lostine, John Day, and Wenaha rivers, Oregon (Starcevich et al. 2005,

TABLE 8. Model selection results for Bull Trout models that were retained in the confidence model set (S = survival; p = recapture probability; k = number of parameters; $QAIC_c$ = quasi-likelihood Akaike's information criterion corrected for small sample sizes; $\Delta QAIC_c = QAIC_c$ difference). States (a–d) are defined in Table 1. Model weights were normalized to sum to 1.0. The submodel for transition probability (Ψ) was the same for both of the top models ($\Psi[\text{state}_{a,b,c,d}]$).

Submodel for S	Submodel for p	Deviance	k	$QAIC_c$	$\Delta QAIC_c$	Model weight	Evidence ratio
$S(\text{Time} + \text{State}_{a,b,c,d})$	$p(\text{Time} + \text{State}_{c,d})$	5,027.2	32	4,953.9	0.00	0.797	1.00
$S(\text{Time} + \text{State}_{a=b,c,d})$	$p(\text{Time} + \text{State}_{c,d})$	5,032.1	31	4,956.6	2.73	0.203	3.93

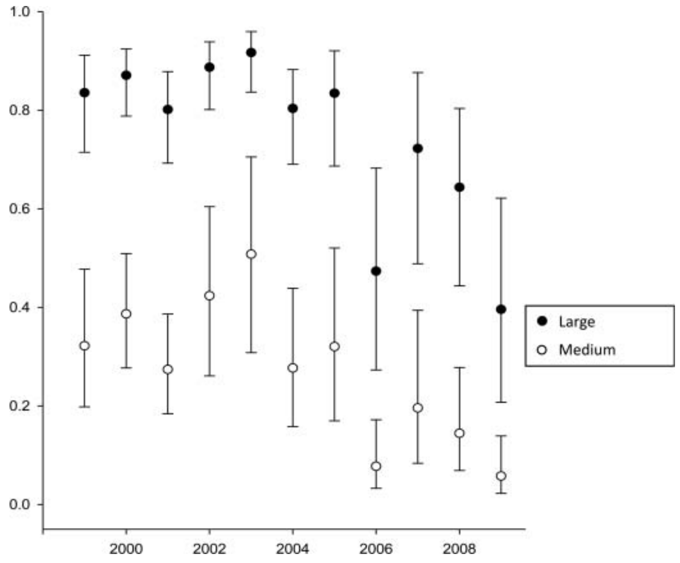

FIGURE 9. Model-weighted estimates (±95% confidence interval) of recapture probability for medium- and large-sized adult Bull Trout, as calculated from the best-approximating multistate capture–recapture model for fish that were tagged in Mill Creek.

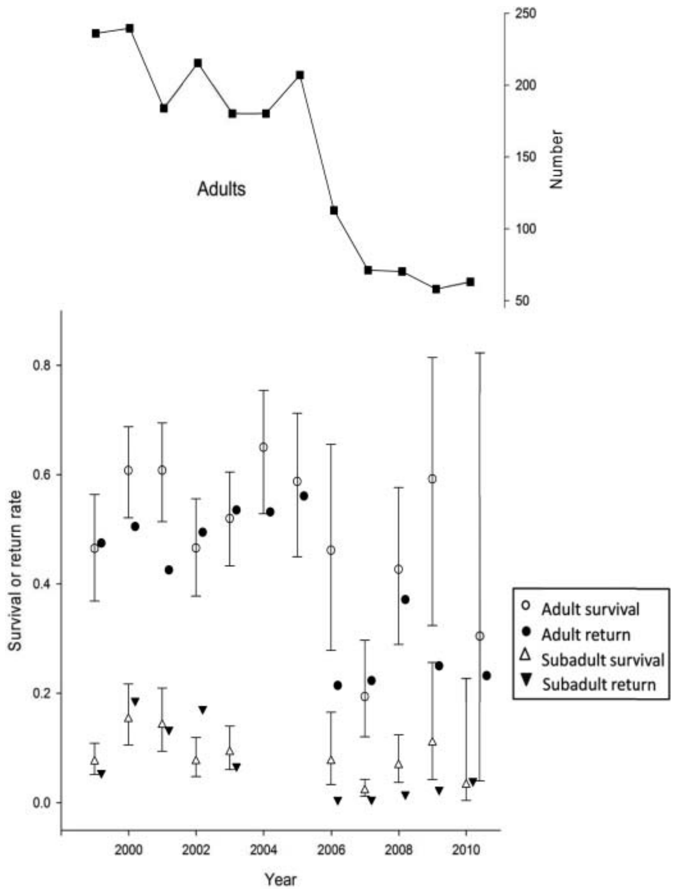

FIGURE 10. Numbers of adult Bull Trout (upper panel) and the return rates and apparent survival rates (±95% confidence interval) of adult and subadult Bull Trout (lower panel) relative to the preceding year, 1999–2010. Annual survival and return rates are offset for clarity.

2012). Mixtures of resident and migratory life histories, including annual variation among individuals, have been noted for other species, particularly salmonids (Hilderbrand and Kershner 2000; McDowall 2001; Schrank and Rahel 2004).

Although the PIT tag data in this study suggested that the intermittently migratory and resident components comprised a small percentage (8%) of the population, other data indicate that they were a larger proportion. In an independent mark–recapture study of adult spawning population size in Mill Creek during 2002–2007, large (≥300 mm FL) adult Bull Trout that resided year-round in the spawning area for at least one annual spawning cycle accounted for, on average, 21% (range = 18–27%) of the total number of adults (Howell and Sankovich 2012). The lower estimates derived from our PIT tag data may be attributable to the screw trap's limitations in recapturing tagged adults of nonmigratory forms due to the trap's location at the lower end of the spawning distribution and its lower efficiency in capturing large fish (Volkhardt et al. 2007), particularly those that exhibit little movement. In the South Fork Walla Walla River, the percentage of

TABLE 9. Subadult and adult return rates (RRs) and apparent survival rates (*S*; 95% confidence interval in parentheses) for Bull Trout that were tagged in Mill Creek, 1998–2004 and 2005–2009. States are further defined in Table 1. Survival was not estimated for small subadults due to the low number of recaptures.

	1998–2004		2005–2009	
State	RR	*S*	RR	*S*
Small subadults			0.003	
Large subadults	0.11	0.11 (0.09–0.15)	0.010	0.05 (0.04–0.07)
Large subadults tagged during March–July	0.09	0.10 (0.08–0.13)	0.01	0.04 (0.03–0.06)
Large subadults tagged during August–February	0.17	0.18 (0.12–0.27)	0.03	0.08 (0.05–0.14)
All adults	0.50	0.55 (0.52–0.58)	0.25	0.34 (0.28–0.40)
Medium adults	0.38	0.44 (0.40–0.48)	0.17	0.25 (0.19–0.31)
Large adults	0.63	0.62 (0.59–0.66)	0.33	0.41 (0.34–0.48)

TABLE 10. Adult return rates (RRs) for PIT-tagged subadult Bull Trout migrating below the PIT antenna arrays in Mill Creek (Kiwanis and Bennington) and Yellowhawk Creek, 2005–2008.

	Subadult migration year			
Variable	2005	2006	2007	2008
Kiwanis array				
Subadults passing array	126	439	294	411
Adult returns	1	1	2	6
Adult RR	0.01	<0.01	0.01	0.02
Bennington array				
Subadults passing array	14	47	19	95
Adult returns	1	1	0	1
Adult RR	0.07	0.02	0.00	0.01
Yellowhawk arrays				
Subadults passing array			21	34
Adult returns			2	0
Adult RR			0.10	0.00

"resident" fish (>420 mm FL; 28%) was similar to our results; however, the percentage of adults that were potentially resident (271–420 mm FL) was larger but decreased with increasing fish size (range = 64–88%). Those resident percentages may be overestimated due to a lack of detection at PIT tag arrays (Al-Chokhachy and Budy 2008). Our long-term data also suggest that some of those apparent resident percentages may be inflated by the shorter duration of the study (i.e., about half of the resident fish were recaptured only once, and some of them may have migrated in other years). Although Mill Creek did contain larger-sized fully resident and intermittently resident adults, no small (<300 mm), mature, potentially resident females were found during systematic sampling conducted throughout main-stem Mill Creek in 2002 (Howell and Sankovich 2012). In that study, we identified what appeared to be a strictly resident Bull Trout population containing only small adults (<200 mm FL) in Low Creek, a Mill Creek tributary. The demographic, life history, genetic, and habitat characteristics of the Low Creek population were very distinct from the characteristics of the adjacent fluvial population in Mill Creek (Howell and Sankovich 2012; P. J. Howell, unpublished data).

TABLE 11. Percentage of PIT-tagged adult Bull Trout overwintering below the PIT antenna arrays in Mill Creek (Kiwanis and Bennington) and Yellowhawk Creek, 2005–2009, that returned to the upstream trap at the Mill Creek intake dam during the subsequent year (RR = return rate).

	Array		
Year and variable	Kiwanis	Bennington	Yellowhawk
2005 downstream adults	27	11	
2006 upstream adults	11	7	
RR, 2006	0.41	0.64	
2006 downstream adults	45	20	
2007 upstream adults	10	7	
RR, 2007	0.22	0.35	
2007 downstream adults	34	20	1
2008 upstream adults	10	10	0
RR, 2008	0.29	0.50	0.0
2008 downstream adults	36	14	4
2009 upstream adults	17	9	1
RR, 2009	0.47	0.64	0.25
2009 downstream adults	45	14	5
2010 upstream adults	17	7	3
RR, 2010	0.38	0.50	0.60
Total downstream adults	187	79	10
Total upstream adults	65	40	4
Total RR	0.35	0.51	0.40

Radiotelemetry has been the most extensively used method to determine Bull Trout distribution (e.g., Dare 2006; Starcevich et al. 2012). Had we relied exclusively on radiotelemetry, the distribution of Bull Trout in Mill Creek would have appeared to extend only as far downstream as Bennington Dam—about 21 km below the intake dam, which is at the lower end of the spawning distribution. Although PIT tag detections also indicated that most of the Mill Creek population's production occurs above Bennington Dam, about 25% of the subadults migrated downstream of Bennington Dam. The PIT tag data also showed that the subadult distribution extended more than 79 km below the intake dam to an area near the mouth of the Walla Walla River; however, none of the fish that were detected in the Walla Walla River survived to return to Mill Creek as adults. Several Bull Trout (155–272 mm FL) that were PIT-tagged in the lower Walla Walla River and that could have originated in Mill Creek were detected at two dams on the main-stem Columbia River: (1) McNary Dam, located 36 km downstream from the mouth of the Walla Walla River; and (2) Priest Rapids Dam, located 132 km upstream of the mouth of the Walla Walla River (Anglin et al. 2010). Similar to the subadult distribution, more than 35% of the adults that were PIT-tagged in upper Mill Creek migrated downstream of Bennington Dam. In addition, some adult-sized Bull Trout that were PIT-tagged in lower Mill Creek below Bennington Dam continued farther downstream into the lower Walla Walla River, passing the Oasis array near the Walla Walla River mouth (Anglin et al. 2010; Ryan Koch, USFWS, unpublished data). Thus, the extent of adult downstream distribution would have been substantially underestimated if based on radiotelemetry data alone, despite the fact that the combined sample size of tagged adults over 3 years represented about 25% of the adult population (a relatively large sample for a telemetry study) during the period of higher abundance. Relative to radio-tagging, PIT-tagging was advantageous in allowing us to tag a larger sample of both subadults and adults over an extended period and to document demographic characteristics and less-frequent but important behaviors.

The combination of radiotelemetry, PIT tag, and mark–resight data indicate that subadult and large adult Bull Trout occupy a continuum of habitats from the headwaters to the lower Walla Walla River and potentially the Columbia River. For subadults in particular, much of this distribution may be occupied year-round. This is contrary to the notion of seasonally occupied migration corridors, which are used primarily to move between spawning/rearing habitat and overwintering habitat (USFWS 2002). This continuous distribution pattern also suggests that the terms "resident" and "migratory" are to some degree an artifact of the demarcation distinguishing the two forms—that is, the lower limit of spawning and juvenile rearing habitat.

Subadult and adult abundances declined substantially below Bennington Dam, where habitat conditions are more highly altered. In Mill Creek and in other Columbia River basin tributaries, the migratory range of radio-tagged adult Bull Trout is more restricted within basins where the lower portion of the watershed is more developed, flow is more heavily diverted, and habitat is more altered (Starcevich et al. 2010). Nevertheless, the more extensive range of PIT-tagged subadults (particularly in lower Mill Creek and the lower Walla Walla River) and the relatively high RR of adults migrating downstream of Bennington Dam demonstrate that for migratory populations whose predominant distribution has contracted upstream, productive capacity could potentially expand if suitable conditions in the lower basin can be restored. The more extensive distribution of Mill Creek subadults is consistent with other char species' migratory, exploratory nature, which is considered an adaptation to exploit food sources (Power 2002). The reduced range of Bull Trout adults may reflect both the lower numbers of subadults in the more distant habitats and the unsuitability of those habitats.

The patterns of subadult and adult distribution were consistent with the summer water temperature patterns. Most of the migratory Bull Trout used habitat that was situated upstream of Bennington Dam, where water temperatures are cooler. Although the adults' migration from below Bennington Dam to upstream areas may reduce their exposure to high temperatures during summer (Howell et al. 2010), that is not the case for most of the subadults that migrate below Bennington Dam. The decline of migratory forms in other Bull Trout populations may be linked to high temperatures and other factors in lower reaches (Nelson et al. 2002).

It has been suggested that migratory behavior in species like the Bull Trout is advantageous for optimizing growth, survival, and reproduction (Northcote 1984; Gross 1991; Jonsson and Jonsson 1993; Power 2002). This may lead to the impression that resident forms are disadvantaged in this regard. However, the diverse Bull Trout life histories evident in Mill Creek appear to help maximize the use of available habitat in Mill Creek and the Walla Walla River to the greater advantage of the species than would be possible with a migratory strategy alone. The dominant migratory pattern allows larger fish to utilize the resources of a larger portion of the system and supports a larger, more fecund population than might be possible in the headwater areas, whereas the exclusive or intermittent residency demonstrated by a smaller portion of the population permits utilization of the headwaters' more limited overwintering capacity and productivity for larger Bull Trout. Small adult Bull Trout occupy small tributaries (e.g., Low Creek) that are not suitable for larger fish. Similarly, a widely dispersed adult winter distribution and a high fidelity to winter locations, which have also been reported in other Bull Trout movement studies (e.g., Bahr and Shrimpton 2004), may help to further reduce competition.

Subadult emigration of fluvial forms has been typified as primarily occurring during spring–summer (McPhail and Baxter 1996). Subadults in Mill Creek generally followed this pattern, with some notable variation. In most years, peak movement of subadults occurred during mid-April to mid-May, whereas in 2006 the peak movement occurred during August. The latter result is similar to that reported for an adjacent Bull Trout population (South Fork Walla Walla River), in which peak downstream movement was consistently observed during August, although sample sizes were relatively small and not adjusted for detection efficiency (Homel and Budy 2008). The late-spring peak movement of subadults in Mill Creek generally coincided with declining flow and increasing water temperature; however, differences in flow patterns among years and exceptional movement during August do not indicate consistent migration cues from these variables. Homel and Budy (2008) likewise saw some influence of temperature on downstream migration in the South Fork Walla Walla River, but most of the variation in movement could not be explained by the environmental variables they modeled, including temperature and discharge. The timing of subadult migration in our study also contrasts with that observed for an adfluvial population in Trestle Creek, a tributary to Lake Pend Oreille, Idaho (Downs et al. 2006): a late-spring pulse of age-1 and older fish was observed during higher flows; and a second, large fall migration occurred as temperatures declined. Although later-migrating (i.e., August–February) subadults survived to adulthood at higher rates in our study, those fish accounted for less than 12% of the subadults during most years except 2006. Thus, the low abundance of later-migrating subadults may limit that survival advantage for the overall population.

Most of the apparent subadult downstream migrants were 126–175 mm and were estimated to be ages 2–3, similar to the age at subadult emigration for other fluvial and adfluvial populations of Bull Trout (Fraley and Shepard 1989; Riehle et al. 1997; Mogen and Kaeding 2005). However, subadult emigrants in Trestle Creek included age-5 fish and a substantial age-4 component (Downs et al. 2006). For Bull Trout in Mill

Creek, the FL at age 3 was similar to that observed in other fluvial populations (Goetz 1989), whereas age-4 subadults were generally smaller in Mill Creek than in other populations. The larger reported lengths at age 3 and especially age 4 for other populations may be attributable to the sampling of subadults that have already migrated and are growing more rapidly. Consistent with the observations of Mogen and Kaeding (2005), we found that age-1 fish had a largely exclusive size-class ($<$125 mm FL), whereas size overlap was greater for age-2–4 subadults (especially ages 3 and 4). The low occurrence of older, larger subadults (176–269 mm FL) in both the screw trap catch and in the systematic sample of Mill Creek upstream of the traps (Howell and Sankovich 2012) also suggests that most subadults migrate downstream at younger ages (age $<$ 4) and smaller sizes.

In 1998–2005, when adult abundance in Mill Creek was relatively high, the upstream-migrating adults arrived at the lower end of their spawning distribution in two pulses: a larger one in mid-July, and a smaller one at the onset of spawning in late August or early September. Larger fish also returned earlier. Oliver (1979) and McPhail and Murray (1979) likewise reported two peaks in adult run timing, but the relative sizes of the peaks and of the adults were reversed: an earlier, smaller peak consisting of smaller fish; and a later, larger peak comprising larger fish. In the South Fork Walla Walla River, only a single, early run was apparent (Contor and Sexton 2003; Homel and Budy 2008). In Mill Creek during 2006–2010 (when abundance declined), adult run timing was later and the return timing for all adult sizes was more uniform. Thus, changes in abundance can be accompanied by shifts in other phenotypic characteristics, such as run timing and size relationships. As a result of the later run timing, a larger proportion of the adult population was exposed to higher temperatures in lower Mill Creek.

Adults in Mill Creek were smaller (mean = 432 mm FL) than adults in adfluvial populations and in several other fluvial populations (mean length = 500–700 mm; e.g., Goetz 1989; Riehle et al. 1997; Stelfox 1997; Swanberg 1997). Like Bull Trout in the South Fork Walla Walla River (Al-Chokhachy and Budy 2008), Mill Creek Bull Trout initially matured at smaller sizes and younger ages (predominantly 3–5 years) than Bull Trout in adfluvial populations (Baxter and Westover 2000; Johnston et al. 2007). Differences in growth patterns relative to other populations were also notable. McPhail and Baxter (1996) described growth spurts in larger, older adults, particularly those in adfluvial populations; such growth spurts have been ascribed to dietary shifts that include larger fish and even small mammals. This was also evident for Bull Trout in Lake Billy Chinook, Oregon, where individuals less than 450 mm primarily consumed smaller Bull Trout and Rainbow Trout, while individuals greater than 450 mm consumed the larger, more abundant kokanee *O. nerka* (Beauchamp and Van Tassell 2001). Growth rates of adults in Mill Creek were considerably lower than those reported for adfluvial adults in the Metolius River/Lake Billy Chinook population (mean = 28–58 mm/year in Mill Creek compared with 156–192 mm/year in the latter population; Riehle et al. 1997) but were similar to the growth rate of adfluvial adults in Trestle Creek (28 mm/year; Downs et al. 2006).

Adult Bull Trout in both fluvial and adfluvial populations can spawn in consecutive years or in nonconsecutive years (McPhail and Baxter 1996; Riehle et al. 1997; Swanberg 1997; Johnston 2005). Riehle et al. (1997) speculated that the consecutive-year spawning of adults in the Metolius River/Lake Billy Chinook population could be related to the rapid growth and recovery of postspawn fish. However, adults in Mill Creek appeared to be almost exclusively consecutive-year spawners despite their considerably slower growth. As in Mill Creek, adfluvial adults in Lake Pend Oreille were largely (83–93%) consecutive-year spawners (Downs et al. 2006). In other adfluvial populations, the proportion of consecutive-year spawners is density dependent (Johnston and Post 2009).

In most cases, estimates of *S* in our study were similar to or slightly higher than RRs, consistent with the results for the South Fork Walla Walla River based on the Barker model (Bowerman and Budy 2012). In all cases, patterns in the RR and survival rate for Mill Creek Bull Trout were similar among the different tag groups. Factors that could negatively bias both types of estimates include permanent emigration of tagged fish from the study area and a lack of detection of large, resident fish in upper Mill Creek above our stationary traps. However, we suspect that the influence of those factors was slight, since the present results as well as our previous results (Howell and Sankovich 2012) indicate that more than 90% of the tagged fish (including migratory and intermittently resident forms) were recaptured in the traps at some point. Our extensive and intensive sampling—which involved trapping essentially all of the migratory spawning adults, mark–resight estimates of marked and unmarked adults above our traps, and PIT tag antenna arrays distributed throughout much of the Walla Walla River basin—suggests a low likelihood that any substantial subadult-to-adult or adult-to-adult survival was not accounted for in our returns.

Estimates of survival and adult returns are rare across the range of Bull Trout populations. Estimates obtained under different trends in adult abundance, estimates of adult recruitment rates, and the use of a long-term data set (which captures more temporal variability) are unique to this study. Two mark–recapture survival studies have been conducted in the South Fork Walla Walla River (Al-Chokhachy and Budy 2008; Bowerman and Budy 2012). The Al-Chokhachy and Budy (2008) study is more comparable to our study in terms of the Bull Trout sizes included and the habitats sampled. Subadult and adult survival rates in the South Fork Walla Walla River during 2002–2005 were similar to those observed in Mill Creek prior to the 2006 decline. During 2002–2005, annual survival rates in the South Fork Walla Walla River averaged 0.09 (SD = 0.05) for 120–170-mm Bull Trout and averaged 0.47 (SD = 0.17) for fish larger than 270 mm. In Mill Creek prior to 2006, the survival rates of large subadults averaged 0.11 (SD = 0.03), while the survival rates of adults averaged 0.56 (SD = 0.07). However, in the South Fork Walla Walla River, there were no differences in survival among adult (>270-mm) size-classes, whereas in Mill Creek, the survival of smaller adults was 29–39% lower than that of large adults. There was no decline in adult survival rate or RR with increasing size or age, even for the largest sizes and oldest age-classes. Estimated *p* for adult Bull Trout tagged in Mill Creek was similar to the relatively high *p* for Bull Trout tagged in the South Fork Walla Walla River.

Differential changes in the Bull Trout survival rate depending on life stage are apparent in Mill Creek and are helpful in assessing life stages that limit the recovery of this population. Although both subadult and adult survival rates decreased with declining adult abundance during 2006–2010, there were substantially greater decreases in subadult-to-adult survival and especially RRs. The subadult RR declined an order of magnitude to 1%, whereas the adult RR declined by 50%. Survival rates showed similar patterns, although the declines in subadult survival and adult survival were less severe. Consequently, the recent decline in adult abundance appears to have been driven more by changes in subadult recruitment to the adult population than by changes in adult survival. The high adult survival rates (particularly during 1998–2005) and adult longevity also indicate the strong potential for adults to continue maintaining the population after their initial recruitment.

Causes of the declines in abundance and survival of Mill Creek Bull Trout are unclear. In the lower reaches of Mill Creek and the Walla Walla River, the habitat used by migratory Bull Trout becomes progressively degraded from agricultural and urban development, flood control channel alterations, and irrigation withdrawals, resulting in reduced habitat quantity and quality (NPCC 2004; Al-Chokhachy and Budy 2008). Low summer flows and high water temperatures are two primary concerns. Al-Chokhachy and Budy (2008) speculated that high flows could lead to lower survival for resident forms in the upper watershed. High flows could also decrease the survival of potential subadults in those reaches. However, in Mill Creek, there was no evidence of flow or temperature changes that could have generated lower subadult and adult survival rates in 2006–2009. Despite degraded habitat conditions in the lower watershed, migratory adult survival was relatively high, especially prior to 2005. Surprisingly, survival rates during the same period were substantially higher for migratory Bull Trout than for nonmigratory fish remaining in the upper South Fork Walla Walla River, which—like upper Mill Creek—contains high-quality habitat (Al-Chokhachy and Budy 2008). Thus, although the habitat conditions in lower Mill Creek and the Walla Walla River may help to explain the low number of subadults using those habitats and the low number of adults produced there, the habitat conditions do not explain the recent declines in survival and adult abundance. Efforts to remedy some of those habitat problems (e.g., by increasing summer flows in the lower Walla Walla River) have also been made in recent years.

The only aspect of our methods that changed in 2005–2010 was the use of 23-mm PIT tags in larger subadults and in adults. Previous studies have found associations between PIT-tagging and increased mortality for juvenile spring Chinook Salmon that received 12-mm tags (Knudsen et al. 2009) and for juvenile steelhead (73–97 mm) that received 23-mm tags (Bateman and Gresswell 2006). However, some of the increased mortality may be related to fish size at tagging. For example, the use of 23-mm PIT tags had no significant effect on Atlantic Salmon *Salmo salar* larger than 90 mm (Zydlewski et al. 2001), Coho Salmon *O. kisutch* larger than 100 mm, or steelhead larger than 100 mm (Zydlewski et al. 2003). We initially limited the application of 23-mm tags to fish that were at least 140 mm FL, and we later increased the minimum size limit to 150 mm FL. When we compared groups of similarly sized subadults (140–150 mm)—one group tagged with 12-mm tags ($N = 301$) and the other group tagged with 23-mm tags ($N = 572$)—rates of survival to adult return during that period were similar (0.33% and 0.35%, respectively). Thus, it is unlikely that the switch to a larger PIT tag size for larger subadults contributed to the decline in subadult survival. Bowerman and Budy (2012) also found no evidence to indicate that PIT-tagging affected the survival of juvenile Bull Trout.

Although the causes of the Bull Trout's decline in Mill Creek are unknown, this decline is consistent with trends in other populations within the region (David Crabtree, USFS, unpublished data). This regional synchrony in abundance suggests that either potentially shared larger-scale factors may be related to the decline or that independent causes in individual basins are occurring simultaneously.

Long-term studies such as this provide an opportunity to describe characteristics of populations, particularly those of long-lived species like the Bull Trout, that is frequently not possible through short-duration studies. For example, we were able to document population attributes that varied with changes in abundance as well as unique and subtle life history differences that are important in characterizing the diversity of the population. The present study and complementary studies in the South Fork Walla Walla River (e.g., Al-Chokhachy and Budy 2008; Homel and Budy 2008; Bowerman and Budy 2012) provide a detailed picture of neighboring Bull Trout populations that is unavailable for most other areas of the species' range.

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