Demographic Characteristics, Population Structure, and Vital Rates of a Fluvial Population of Bull Trout in Oregon

ROBERT AL-CHOKHACHY* AND PHAEDRA BUDY

U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit,
Department of Watershed Sciences, Utah State University, Logan, Utah 84322-5210, USA

Abstract.—Identification of the factors limiting inland salmonid populations, such as those of the threatened bull trout *Salvelinus confluentus* in the Pacific Northwest, can be particularly challenging due to substantial gaps in our understanding of population demographics, population structure in the presence of multiple life history forms, and vital rates. We implemented a large-scale mark–recapture program over a 5-year period using an innovative combination of active and passive techniques to estimate (1) bull trout age and growth by size-class, (2) the proportion of the population exhibiting resident and migratory behavior, and (3) survival rates (*S*) for different life stages and life history forms (resident and migratory). Our results suggest that bull trout reached sexual maturity at a relatively small size (200 mm) and young age (3–4 years) and that large individuals (>600 mm) can reach ages greater than 12 years in this fluvial population. Using active and passive mark–recapture methods, we found that large bull trout (>420 mm) were predominantly migratory in behavior (72% were migratory) and that there was considerable variability among other size-classes in the proportion exhibiting migratory behavior. Survival rate varied significantly across size-classes and study years. Juvenile bull trout (120–170 mm) exhibited the lowest annual *S* on average (0.09) and the highest interannual variability (coefficient of variation = 0.60) in *S* among size-classes. Fish exhibiting migratory life history patterns generally had higher *S* than did resident fish; small, juvenile residents had a significantly mean *S* (0.15; SE = 0.02) than did similarly sized migratory fish (mean *S* = 0.35; SE = 0.04). Collectively, our results highlight important differences across life history forms within and across populations; these factors must be considered when designing future recovery and management strategies for any single bull trout recovery unit or across larger geographic areas.

The design of sound recovery and management strategies for fish populations requires an understanding of life stages that limit overall population growth and persistence (Wilson 2003; Legault 2005). Identification of limiting life stages often involves the use of population models (Stearns 1992), which require explicit demographic and vital rate information. However, obtaining this information can be temporarily and monetarily challenging and extremely difficult when populations exhibit multiple life history forms, low abundance, and high variability in demographic processes (Al-Chokhachy 2006; Homel and Budy 2008). Nevertheless, this information is necessary for providing a framework to assess the relative effects of various management options, such as harvest practices (e.g., Crowder et al. 1994), restoration efforts (e.g., Hilderbrand 2003), and management scenarios (e.g., Marschall and Crowder 1996).

A sound understanding of population dynamics, demographics, and vital rates is critical to planning effective conservation strategies for bull trout *Salvelinus confluentus*, a species of char that is native to the Pacific Northwest and Canada and that has been listed as threatened under the Endangered Species Act in the United States since 1998 and as a species of special concern in Canada since 1995. Across their native range, bull trout have exhibited substantial declines in population abundance and distribution as a result of habitat degradation and fragmentation (Fraley and Shepard 1989; Rieman and McIntyre 1995; Ripley et al. 2005) and the introduction of nonnative species (Leary et al. 1993). Bull trout are known to exhibit multiple life history forms including anadromous, fluvial, and adfluvial; multiple forms can coexist within a single population (Rieman and McIntyre 1993; Nelson et al. 2002; Homel and Budy 2008). As in many other salmonid populations (e.g., Bonneville cutthroat trout *Oncorhynchus clarkii utah*; Colyer et al. 2005), the migratory component of many bull trout populations has declined significantly (Nelson et al. 2002). As a result, bull trout exist only as subpopulations across the range of their former distribution (Rieman et al. 1997). Bull trout are also known to be generally associated with complex habitats (Muhlfeld and Marotz 2005; Al-Chokhachy and Budy 2007) and to occur in naturally low densities (Rieman and McIntyre 1993). These attributes, in conjunction with the diverse life history strategies, can result in

* Corresponding author: robert.a@aggiemail.usu.edu

problematic sampling and monitoring of bull trout populations (Al-Chokhachy 2006).

Despite the listing and current status of bull trout, there are significant gaps in our understanding of bull trout population dynamics and critical vital rates. In particular, there are few empirical estimates of survival rate (S), and estimates of S that are specific to life stages or life history forms are generally lacking. Additionally, the majority of bull trout research has focused on the migratory individuals from adfluvial populations where migratory and resident fish are easily delineated (e.g., Fraley and Shepard 1989). As such, our understanding of the structure of populations where multiple life history forms coexist is extremely limited but is fundamental for future management actions. Overall, there is little information describing demographic characteristics, S, growth, fecundity, and population structure of fluvial bull trout populations. These data gaps limit (1) our understanding of bull trout ecology, (2) our ability to complete formal population viability analyses, and (3) assessments of the effects of different management scenarios on bull trout populations.

In this study, we used 5 years of comprehensive mark–recapture data to evaluate demographic and vital rate information for a fluvial population of bull trout. Our approach is unique, as we combined active capture–recapture data from annual summer sampling and year-round, continuous recapture data from passive instream antennae (Zydlewski et al. 2006) to maximize our understanding of bull trout vital rates and structure in a population containing resident and migratory life history expressions. Within this framework, our specific objectives were to (1) estimate bull trout S and factors affecting S across multiple size-classes; (2) evaluate potential differences in vital rates across life history forms; (3) quantify bull trout age structure and fecundity; and (4) evaluate the proportion of the population exhibiting migratory behavior. Our estimates of key vital rates and their variability provide critical insight into the ecology and population dynamics of this imperiled species and can aid in identifying factors that limit bull trout populations across the species' native range.

Methods

Study area.—We completed a detailed mark–recapture study on the South Fork Walla Walla River (SFWWR; 2002–2006) in northeastern Oregon (Figure 1). The SFWWR originates in the Blue Mountains at the eastern boundary of the arid steppe of the Columbia River basin and is characterized by hot, dry summers and cold, wet winters. Despite the relatively low elevation (610–1,000 m) of the SFWWR study site,

cold groundwater influences maintain regular base flow conditions (base flow discharge = 2.6 m³/s) and regulate water temperature such that it does not exceed 16°C (Budy et al. 2005); thus, water temperature was probably not a limiting factor during this study (Selong et al. 2001). Habitat conditions within the SFWWR can generally be described as high quality and subject to few forest management activities; however, recreational activities (e.g., hiking) do occur throughout the drainage. Downstream of the SFWWR, habitat conditions degrade longitudinally as water temperature, habitat simplification, channelization, and migration barriers increase.

The SFWWR is located primarily in the Umatilla National Forest and is approximately 21 km in length. We divided the SFWWR into 200-m sample reaches (102 reaches total, average width = 10 m) and used a systematic sampling design (based on an annual 20% minimum sampling rate) to achieve spatial balance in sampling (Stevens and Olsen 2004). Under this approach, our sample reaches were distributed throughout our study site (~1-km intervals between reaches), which enabled us to effectively sample across the headwater reaches, where the majority of spawning occurs, and to sample resident and migratory adults in the reaches farther downstream (Budy et al. 2003).

The fish assemblage within the SFWWR consisted primarily of rainbow trout *O. mykiss,* steelhead (anadromous rainbow trout), Chinook salmon *O. tshawytscha*, mountain whitefish *Prosopium williamsoni*, and sculpins *Cottus* spp. The SFWWR is known to contain a relatively large population of both small (potentially resident) and large (potentially migratory) bull trout (Al-Chokhachy et al. 2005); the abundance of bull trout larger than 120 mm was recently estimated at 10,600 fish (95% confidence interval [CI] = 8,800–16,598 fish; Budy et al. 2007a). The SFWWR did not contain brook trout *S. fontinalis*, which are nonnative competitors of bull trout that have been introduced throughout much of the Pacific Northwest.

Mark–recapture data.—We initiated our mark–recapture efforts in 2002 in the SFWWR; annual sampling began in mid-June and continued until the first week of August. This sampling period generally occurred before the downstream migration of juvenile bull trout from the SFWWR (Homel and Budy 2008) and after the upstream movements of migratory bull trout (Contor et al. 2003; Homel and Budy 2008). Each year, we sampled all selected reaches once using multiple techniques to actively capture and recapture bull trout. To avoid potential sampling bias across size-classes and habitat types, we used a combination of techniques, including snorkeling to corral fish into trap nets, electroshocking downstream to a seine, and
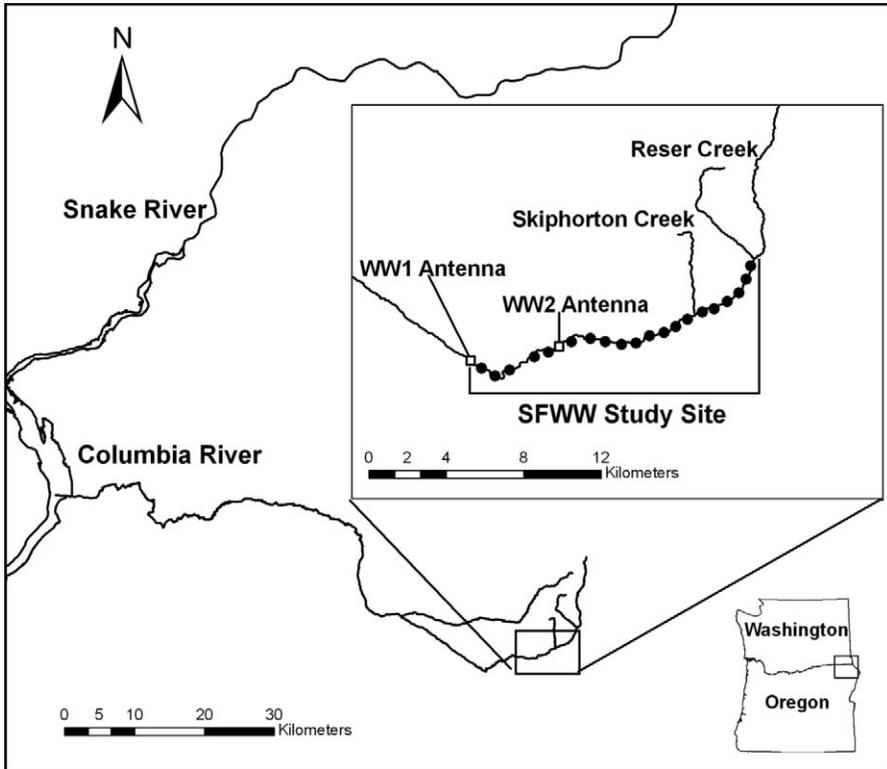
FIGURE 1.—Map of the South Fork Walla Walla River study site in northeastern Oregon, illustrating the locations of two passive integrated transponder (PIT) tag antennae (WW1 and WW2; open squares) and the approximate distribution of sampling reaches (black circles) used to evaluate bull trout age, growth, life history expression, and survival.

angling (Williams et al. 2002; Budy et al. 2003). Upon capture, every bull trout larger than 120 mm was anesthetized, tagged with a year-specific external anchor tag, and given a 23-mm passive integrated transponder (PIT) tag that was surgically implanted (~5-mm incision) in the ventral cavity anterior to the pectoral fins. Double tagging of individuals allowed us to quantify tag retention rates and to estimate the probability of misidentifying a previously tagged individual. After receiving tags, the fish were weighed, measured, and released at the point of capture. Recaptured individuals were anesthetized, checked for tag loss (both anchor and PIT tags), weighed, measured, and released.

Passive PIT tag antennae (hereafter, antennae) were installed in the SFWWR to provide additional recaptures and quantify movement. Two antennae were installed in fall 2002: one (WW1) was located at the downstream end of the study site, and the other (WW2) was situated approximately 6 km upstream from WW1 (Figure 1). Each antenna consisted of rectangular polyvinyl chloride detectors that spanned the entire stream width.

Although our antennae were in place since their deployment in 2002, overall detection efficiency of the antennae was a function of two separate factors. First was the efficiency of detecting a tagged fish that passed through the antennae; this type of efficiency can vary as a result of occasional environmental disturbances (e.g., high-water events) and has been estimated at 80–100% (2004–2005; Homel and Budy 2008). Second, there were short time intervals over which an individual antenna was shut down due to technical difficulties; detection efficiency for these periods was estimated from tagging location information (Global Positioning System data) and antenna recaptures. For example, if a fish tagged upstream from WW2 was detected at WW1 but not at WW2, we recorded a missed detection at WW2, and so on. From this analysis, we estimated overall detection efficiency at the SFWWR antennae to be 50% over the course of this study (Homel and Budy 2008). Nevertheless, while reduced detection efficiency at our antennae may have affected our assessment of population structure, this factor should have minimal effects on our analyses of S, as these types of open mark–recapture models

estimate capture probability and account for it in the estimation of S.

Age and fecundity.—Each year (2002–2006), we sacrificed up to 10 bull trout from the SFWWR for quantification of age structure and variability in length at age, evaluation of age and length at sexual maturity, and estimation of the length–fecundity relationship. We collected fish across all size-classes (except young of the year) during the first week of August to observe maximum egg development in females. We enumerated all eggs from mature females and collected the sagittal otoliths from each fish. We used two independent observers and a dissecting microscope for aging. Since field observations from snorkel surveys indicated that large bull trout exist in the SFWWR (>620 mm; Budy et al. 2005), we also used a von Bertalanffy length-at-age model to estimate the potential age of these large individuals (multiplicative error model; Quinn and Deriso 1999).

Survival analyses.—We used the Barker model in Program MARK (White and Burnham 1999) to estimate S for the SFWWR population; this open mark–recapture model incorporates capture–recapture data from individual sampling occasions and recapture data between sampling occasions, thus improving the precision of S estimates over models that only incorporate recapture data from sampling occasions (e.g., the Cormack–Jolly–Seber model; Barker 1999). In addition to S, the Barker model also allows estimation of recapture probability (p); the probability of resighting a dead animal (r); the probability of recapturing an animal between sampling intervals (R); the probability of recapturing an animal before the animal dies between sampling intervals (R'); the probability that an animal at risk of capture in time t is also at risk of capture in time $t + 1$ (F); and the probability that an animal not at risk of capture in time t is at risk of capture in time $t + 1$ (F').

We used 5 years of mark–recapture data for these analyses, and we separated each year into two intervals. Interval 1 corresponded to summer field sampling ($\sim$June 15–August 15) and included active captures and recaptures (i.e., electroshocking) as well as all antenna recaptures. Interval 2 corresponded to the interval between the sampling periods (August 16–June 14) and included only the antenna recaptures. Average growth rates calculated from individual recapture data were used to create a stage-based model for six size-classes (121–170, 171–220, 221–270, 271–320, 321–370, and >370 mm) determined from previous bull trout length-at-age analyses (Budy et al. 2003).

We performed two separate mark–recapture analyses for bull trout in the SFWWR. First, we evaluated S across the previously mentioned size-classes. Here, we established a set of a priori models that included group (size-class) and time effects, and we considered relative condition (C) at the time of tagging as an individual covariate. We calculated C for the SFWWR population as

$$C_i = w_i / l_i^{(3.06 \times 0.000006)},$$

where C_i is the relative condition of individual i, w_i is fish weight at tagging, and l_i is fish total length at tagging. For the second set of analyses, we evaluated the difference in vital rates between fish exhibiting resident and migratory life history patterns. In these analyses, we considered any fish that moved below WW1, the lowermost antenna, to be migratory (see next section) and all other fish to be resident. For analyses of life history forms, the a priori models included group, life history expression (resident or migratory), and time.

We used Program MARK to generate the likelihood function value for each model and to estimate Akaike's information criterion corrected for small-sample bias (AIC$_c$; Burnham and Anderson 1998). For all analyses, models were ranked according to the lowest AIC$_c$ score, and the difference in AIC$_c$ values (ΔAIC$_c$) between models was used to calculate an Akaike weight (W_i) for each model (Burnham and Anderson 1998). Although the models were ranked according to the lowest AIC$_c$ score, we used model averaging for parameter estimates (i.e., S) to maximize the information gained within a multimodel approach (Burnham and Anderson 1998). We fixed r equal to zero, as there was an extremely low probability of recapturing a dead fish. We initially modeled F and F' separately and then considered models where F was equal to F'; this allowed us to evaluate (using AIC$_c$ scores) whether immigration or emigration was random (i.e., $F = F'$) or directional (i.e., $F \neq F'$) in the SFWWR. Similar to Franklin et al. (2000), we first modeled those parameters that were less pertinent to our analysis (F, F', R, R', and p); we then maintained the model structure of those parameters from the highest-ranking model (i.e., lowest AIC$_c$) while modeling S. All a priori S models were compared based on AIC$_c$ scores; the model with the lowest AIC$_c$ score that was at least 2 points less than the next-lowest AIC$_c$ score (i.e., ΔAIC$_c$ ≥ 2) was considered the most plausible (Burnham and Anderson 1998).

We used the likelihood function in Program MARK to estimate the slope (β) for all parameters, and the logit link function was used to transform β estimates into real estimates of S. We used the 95% CI as an index of statistical significance for each parameter. To avoid type II error from overly conservative CIs (Tyron 2001), we recalculated the 95% CIs for any two

TABLE 1.—Total number of bull trout tagged in each size-class (total length) percentage of the total number of tagged fish contributed by each size-class, average (SE in parentheses) annual growth (mm) of fish that were actively recaptured during mark–recapture sampling, and percentage of fish exhibiting migratory behavior within each size-class in the South Fork Walla Walla River, Oregon, 2002–2006. Migratory percentages were expanded by estimates of antenna detection efficiency (see Methods).

Size-class	Number tagged	Percent of total	Annual growth	Migratory (%)
121–170	928	52.1	53.6 (8.2)	12.1
171–220	326	18.3	71.1 (7.6)	23.3
221–270	171	9.6	52.8 (7.2)	19.9
271–320	84	4.7	37.1 (7.4)	11.9
321–370	71	4.0	25.6 (7.0)	14.1
371–420	78	4.4	19.9 (2.2)	35.9
>420	122	6.9	15.1 (2.7)	72.1

FIGURE 2.—Mean (+2SE) annual length frequency distribution (total length) of passive integrated transponder tagged bull trout and bull trout observed during snorkel surveys in the South Fork Walla Walla River, Oregon, from 2002 to 2006.

comparisons as:

$$\beta_x \pm t(\bar{E}) \times SE_x,$$

where $E = (\sqrt{SE_x^2 + SE_y^2}/(SE_x + SE_y)$ and where β_x is the estimate for group x, $\bar{E}$ is the average of E-values across all pairwise combinations, SE_x is the standard error for group x, SE_y is the standard error for group y, and t is the t-value (set at 1.96 for all groups). We considered differences among parameter estimates to be significant when the 95% CIs did not overlap with those of comparable groups.

Since formal goodness-of-fit tests are not valid when individual covariates are modeled in mark–recapture analyses (Cooch and White 2005), we evaluated potential sources of model error using supplemental information independent of Program MARK. Specifically, we used active capture–recapture data to evaluate the percentage of fish that lost their PIT tags and the percentage that lost anchor tags; we multiplied these two estimates to produce an overall estimate of the probability of misidentifying a tagged fish as unmarked. In addition, we assessed potential size bias in capture methods by comparing the average length frequency distribution from capture data with that from snorkel data collected in similar sample reaches in the SFWWR (see Al-Chokhachy et al. 2005 and Al-Chokhachy 2006 for more detail on snorkel methods).

Migratory proportion estimate.—We used active marking and recapture data and passive recaptures at antennae to estimate the percentage of the SFWWR population that exhibited migratory behavior. Any bull trout that moved below WW1, which corresponded to a distance of over 12 km from the downstream limit of the core spawning area, was considered to be a migratory individual (Homel 2007). We estimated the proportion of each size-class that exhibited migratory behavior as:
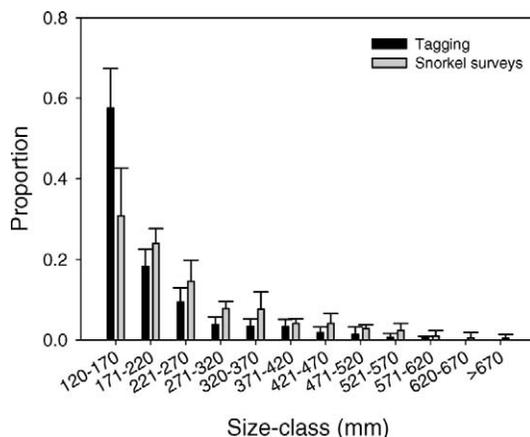
$$\text{Proportion migratory}_s = (m_s/t_s)/a_e,$$

where s represents size-class, m_s is the number of individuals in a particular size-class that moved below WW1, t_s is the total number of marked individuals in a particular size-class, and a_e is antenna efficiency (50%).

Results

From 2002 to 2006, we marked 1,780 individual bull trout, observed unique recaptures for 412 individuals, and recorded 713 total recaptures in the SFWWR (Table A.1). The size distribution of bull trout was dominated by smaller, potentially immature bull trout; 70% of the fish sampled were smaller than 220 mm (Table 1; Figure 2). Our recapture data suggest that bull trout growth rates were relatively consistent up to 270 mm, at which growth declined consistently with increasing size.

Age and Fecundity

Based on otolith aging techniques, bull trout appeared to be relatively long lived in the SFWWR; the maximum age observed in the subset of sacrificed fish was 9 years (Figure 3a). Age was estimated for a total of 33 individual bull trout across a wide range of fish lengths (98–564 mm), and there was considerable variability in length at age for fish larger than 250 mm (Figure 3a). The highest variability occurred in age-5 fish, which ranged from 292 to 452 mm. Juveniles and small adults (<220 mm), however, exhibited little
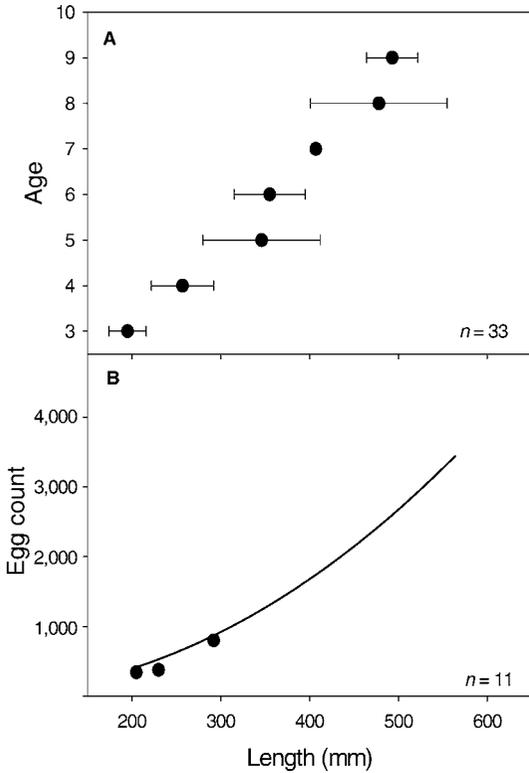
FIGURE 3.—Relationship between bull trout total length (mm) in the South Fork Walla Walla River, Oregon (2002–2006), and **(a)** age (males and females) or **(b)** fecundity (number of eggs/female; $y = 0.0013x^{2.34}$, where $y =$ fecundity and $x =$ length; $R^2 = 0.95$).

variability in length at age. The von Bertalanffy results ($F_{33} = 166.93$, $P \leq 0.0001$) suggested that large bull trout (observed in snorkel surveys) in the SFWWR can reach 12 years of age:

$$L = 2.308[1 - e^{-0.00254(t+0.462)}],$$

where L is the length of the fish, t is age, and e is the base of natural logarithms.

During the study, we were only able to obtain fecundity data from 11 sacrificed mature individuals. Based on examination of these individuals, bull trout in the SFWWR appeared to achieve sexual maturity at approximately 200 mm or at age 3–4 (Figure 3b). The number of eggs increased significantly with size, yielding the following relationship between length and fecundity (df $= 9$, $R^2 = 0.95$):

$$y = 0.0013x^{2.34},$$

where y is the number of eggs per female and x is fish length.

Mark–Recapture Analyses

Survival.—Based on our analyses of bull trout S, the top model included size-class (group) and time, and C was an individual covariate modeled as an interaction across size-classes and time periods ($W_i = 66.3\%$; Table 2). We observed significant differences in model-averaged estimates of bull trout S across size-classes (Figure 4A–F). In particular, 120–171-mm fish exhibited significantly lower S than all other size-classes (Figure 4A); in contrast, S did not differ significantly across all other size-classes. Our top-three models (total $W_i = 96.7\%$) included time as an additive parameter, where the differences in S across groups were consistent over the course of the study (Table 2), and we found little evidence of interaction effects (i.e., group × time; $W_i = 3.3\%$; Table 2). We observed significantly lower S in 2004 (across all size-classes) than in all other study years (Figure 4). Our top model included C modeled as an interactive effect with size-class (Table 2). However, our results suggested that C only significantly affected the model fit for juvenile bull trout S (120–170 mm size-class, $\beta = 5.60$, SE $= 2.09$), whereas it did not affect the model fit of S for fish larger than 170 mm.

The top model identified from life history form analyses suggested that bull trout S differed between migratory and resident fish ($W_i = 98.2\%$; Table 3). For these analyses, we used results from size-class analyses (i.e., differences in S across groups) and size-class-specific information about movement (percentage of fish exhibiting the migratory life history pattern in a given size class; see next section) to combine fish into three size-classes (120–170, 171–320, and >320 mm). Similar to the previous analyses, S varied across time, and the lowest annual estimates of S were observed in 2004. Bull trout exhibiting migratory movement patterns had higher S across size-classes (Figure 5A–C), but only the small (120–170-mm) migratory fish (average $S = 0.35$, SE $= 0.04$) exhibited significantly higher S than similarly sized resident fish (average $S = 0.15$, SE $= 0.02$).

Capture.—In size-class analyses, capture rate differed by size-class and time (Table 4), and we observed relatively high variability in capture rate for each size-class (Table 4). Capture rates for 171–220-mm bull trout were significantly lower than those for bull trout exceeding 370 mm, but no significant difference was observed for any other size-class comparison (Table 4). The probability R varied by group and time; the highest value was observed for bull trout larger than 370 mm (average $R = 0.50$, SE $= 0.05$), and the lowest value was observed for 271–320-mm fish (average $R = 0.13$, SE $= 0.02$); this pattern was consistent with our antenna
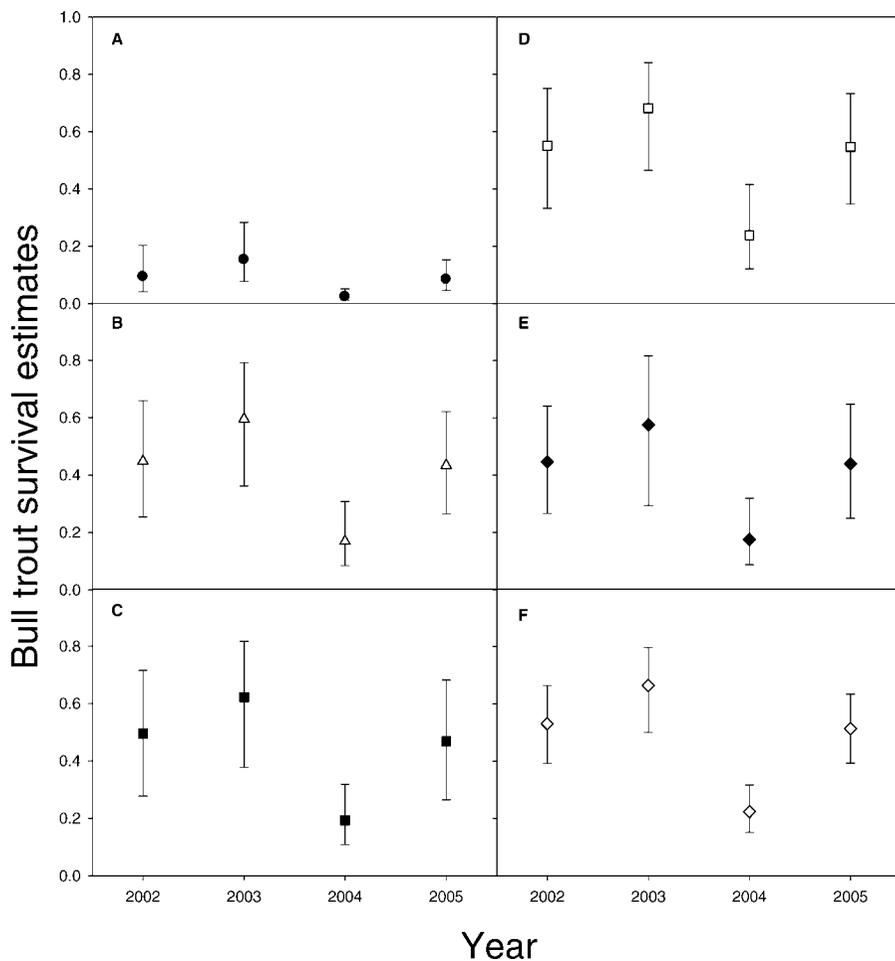
FIGURE 4.—Estimates of survival rate ($\pm 95\%$ confidence interval) calculated from mark–recapture analyses of six bull trout size-classes (total length) in the South Fork Walla Walla River, Oregon, 2002–2005: **(A)** 120–170 mm, **(B)** 171–220 mm, **(C)** 221–270 mm, **(D)** 271–320 mm, **(E)** 321–370 mm, and **(F)** larger than 370 mm .

TABLE 2.—Summary of model selection among Barker mark–recapture models used to estimate bull trout survival rate (S) across size-classes in the South Fork Walla Walla River, Oregon, 2002–2006 (g = group or size-class; t = time; C = relative condition; period symbol = no difference across time or among size-classes; $+$ = additive parameter; $\times$ = interaction effect). The Barker model includes six parameters: S; capture probability (p); probability of recapturing a fish between sampling occasions (R); probability of recapturing a fish before it dies between sampling occasions (R'); probability that a fish at risk of capture in time t is also at risk of capture in time $t+1$ (F); probability that a fish not at risk of capture in time t is at risk of capture in time $t+1$ (F'); and probability of resighting a dead animal (r), which was fixed to equal 0. Akaike's information criterion corrected for small-sample bias (AIC_c), Akaike weight (W_i), and likelihood of each model are shown.

S varies by	Model	AIC_c	W_i	Model likelihood
g, t as an additive parameter, c as an interactive parameter with g	$S_{[g+t+(c \times g)]} p_{(g+t)} R_{(g+t)} R'_{(g+t)} F'_{(.)} F'_{(.)}$	3,284.8	0.633	1.000
g, t as an additive parameter	$S_{(g+t)} p_{(g+t)} R_{(g+t)} R'_{(.)} F_{(.)} F'_{(.)}$	3,286.7	0.245	0.388
g, t, and c as an additive parameters	$S_{(g+t+c)} p_{(g+t)} R_{(g+t)} R'_{(g+t)} F_{(.)} F'_{(.)}$	3,288.8	0.089	0.141
g, t as an interactive parameter	$S_{(g \times t)} p_{(g+t)} R_{(g+t)} R'_{(g+t)} F_{(.)} F'_{(.)}$	3,290.8	0.032	0.051
g, t as an interactive parameter (p varies as an interaction with t)	$S_{(g \times t)} p_{(g \times t)} R_{(g+t)} R'_{(g+t)} F_{(.)} F'_{(.)}$	3,302.9	0.000	0.000

TABLE 3.—Summary of model selection among Barker mark–recapture models used to estimate bull trout survival rate (S) for fish exhibiting resident (res) and migratory (mig) behavior in the South Fork Walla Walla River, Oregon, 2002–2006 (g = group, one of three size-classes [120–170, 171–320, and >320 mm total length]; t = time; + = additive parameter; × = interaction effect). Akaike's information criterion corrected for small-sample bias (AIC$_c$), Akaike weight (W_i), and likelihood of each model are shown. See Table 2 for a description of Barker model parameters.

S varies by	Model	AIC$_c$	W_i	Model likelihood
g, t as an additive parameter	$S_{(g+t)}p_{(g+t)}R_{(g \times t)}R'_{(g)}F_{(res,mig)}F'_{(t)}$	2,758.1	0.982	1.000
g (no difference between res and mig), t as an additive parameter	$S_{(g+t;no\ res,mig)}p_{(g+t)}R_{(g \times t)}R'_{(g)}F_{(res,mig)}F'_{(t)}$	2,766.1	0.018	0.018
g, t as an interactive parameter	$S_{(g \times t)}p_{(g+t)}R_{(g \times t)}R'_{(g)}F_{(res,mig)}F'_{(t)}$	2,777.6	0.000	0.000
g (no difference between res and mig), t as an interactive parameter	$S_{(g \times t;no\ res,mig)}p_{(g+t)}R_{(g \times t)}R'_{(g)}F_{(res,mig)}F'_{(t)}$	2,783.2	0.000	0.000
g, t as an interactive parameter; p varies by g	$S_{(g \times t)}p_{(g)}R_{(g \times t)}R'_{(g)}F_{(res,mig)}F'_{(t)}$	2,796.1	0.000	0.000
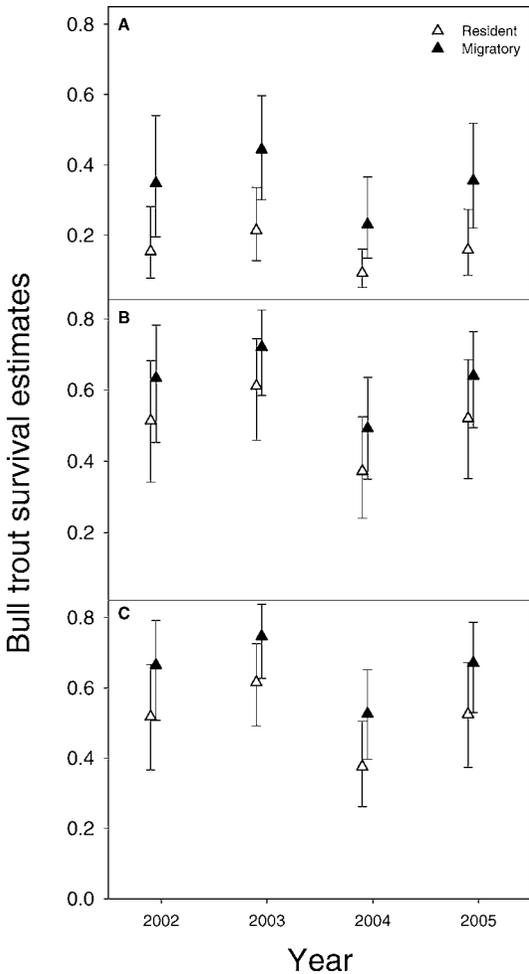
FIGURE 5.—Estimates of survival rate (±95% confidence interval) calculated from mark–recapture analyses of resident and migratory bull trout from three size-classes (total length) in the South Fork Walla Walla River, Oregon, 2002–2005: **(A)** 120–170 mm, **(B)** 171–320 mm, and **(C)** larger than 320 mm.

recaptures during these intervals and with estimates of the proportion of fish exhibiting migratory behavior within a size-class. The R' value also varied by group and time. Similar to results for R, the highest R' was observed for fish larger than 370 mm (average R' = 0.15, SE = 0.04), and significantly lower values were estimated for size-classes between 171 and 320 mm (Table 4).

We observed substantial differences in capture rate between fish exhibiting resident and migratory life history patterns. Capture probability differed across size-classes, life history types, and time periods (Table 5). The estimated p for 120–170-mm migratory fish (average p = 0.77, SE = 0.08) was significantly higher than that for similarly sized resident fish (average p = 0.36, SE = 0.09), but we found no significant difference in comparisons of other size-classes (Table 5). The value of R varied as an interaction between groups (size-classes and life history forms); however, R' varied only across life history forms but not across time. As expected, R and R' values were significantly higher for fish exhibiting migratory movement patterns than for resident fish. This result was consistent across all size-classes except the 120–170-mm size-class, for which R did not differ (Table 5).

Immigration and emigration.—Model selection results from size-class analyses suggested that emigration and immigration were nonrandom during this study (i.e., $F \neq F'$; Table 4). The probability F did not differ by size-class or time, and average F was 0.78 (SE = 0.05), suggesting a relatively high level of emigration. On the contrary, we found very low estimates of F' (average = 0.00; SE was inestimable), indicating very little immigration from other potential local populations.

Life history form analyses suggested a similar pattern of nonrandom immigration (Table 5). Estimates of F did not vary by size-class but did vary by life history form, and F was significantly higher for bull

TABLE 4.—Model-averaged estimates (SE in parentheses) of six parameters (defined in Table 2) from Barker mark–recapture models used to estimate survival rates of six bull trout size-classes (total length) in the South Fork Walla Walla River, Oregon, 2002–2006.

Size-class (mm)	p	R	R'	F	F'
120–170	0.41 (0.11)	0.25 (0.03)	0.07 (0.03)	0.80 (0.05)	0.00 (na)
171–220	0.20 (0.07)	0.23 (0.03)	0.05 (0.01)	0.80 (0.05)	0.00 (na)
221–270	0.39 (0.11)	0.17 (0.02)	0.02 (0.01)	0.80 (0.05)	0.00 (na)
271–320	0.57 (0.11)	0.13 (0.02)	0.05 (0.02)	0.80 (0.05)	0.00 (na)
321–370	0.61 (0.11)	0.36 (0.04)	0.08 (0.02)	0.80 (0.05)	0.00 (na)
>370	0.75 (0.09)	0.50 (0.05)	0.15 (0.04)	0.80 (0.05)	0.00 (na)

trout exhibiting migratory movement ($F = 0.85$, SE = 0.07) than for resident fish ($F = 0.36$, SE = 0.09). Although variable, we observed no differences in F' between life history forms ($F' = 0.31$, SE = 0.16).

Goodness of fit.—We found potential evidence for violations of mark–recapture assumptions in our data (but see Discussion). In particular, we observed substantial differences in length frequency distribution between bull trout observed during snorkel surveys and those captured for mark–recapture analyses. Our results indicated that we captured small (120–170-mm) juvenile bull trout in a higher proportion than was observed during snorkel surveys (i.e., positive sample bias), but no substantial difference between methods was observed for the other size-classes (Figure 5). However, we did not find any indication of tag loss. Specifically, PIT and anchor tag retention rates were 93% and 85%, respectively; the probability of a fish losing both tags and thus being misidentified was 1%.

Migratory Proportion of the Population

In the SFWWR, individuals from all bull trout size-classes (>120 mm) exhibited migratory movements (i.e., moved below WW1; Table 1). The highest percentage (72.1%) of migratory behavior was observed in bull trout larger than 420 mm, and relatively high (35.9%) migratory behavior was exhibited by 371–420-mm fish. The percentage of all juveniles or small adults expressing migratory behavior was relatively low (range = 11.9–23.3%), but the high numbers of fish in these smaller size-classes (particularly 120–220 mm) indicate that a substantial number of fish in the SFWWR are migratory.

Discussion

Field estimates of key demographic and vital rates can provide valuable insight into the dynamics of the population of interest and can increase our understanding of other conspecific populations for which limited information is available (Crowder et al. 1994; Williams et al. 2002). In this investigation, we used 5 years of mark–recapture sampling and field techniques to quantify critical components for evaluating bull trout population viability and persistence, including demographic and vital rates. Additionally, we quantified the population structure of a fluvial bull trout population that contained both resident and migratory fish (Al-Chokhachy et al. 2005). With our results, we address substantial gaps in the current understanding of bull trout biology and provide a template for future bull trout research and recovery efforts.

Demographic and Vital Rates

Across their native range, bull trout can exhibit multiple life history forms, suggesting that discrete differences in demographic and vital rates exist between forms. Furthermore, while much of our current knowledge of bull trout population demographics has come from adfluvial populations (e.g., Fraley and Shepard 1989), many of the populations through-

TABLE 5.—Model-averaged estimates (SE in parentheses) of six parameters (defined in Table 2) from Barker mark–recapture models used to estimate survival rates of bull trout exhibiting resident and migratory behavior (three size-classes [total length] within each life history type) in the South Fork Walla Walla River, Oregon, 2002–2006.

Size-class (mm)	p	R	R'	F	F'
Resident					
120–170	0.36 (0.09)	0.14 (0.12)	0.04 (0.01)	0.36 (0.09)	0.31 (0.16)
171–320	0.49 (0.10)	0.06 (0.04)	0.03 (0.02)	0.36 (0.09)	0.31 (0.16)
>320	0.73 (0.08)	0.26 (0.12)	0.00 (0.04)	0.36 (0.09)	0.31 (0.16)
Migratory					
120–170	0.77 (0.08)	0.28 (0.11)	0.88 (0.05)	0.85 (0.07)	0.31 (0.16)
171–320	0.47 (0.10)	0.32 (0.10)	0.94 (0.05)	0.85 (0.07)	0.31 (0.16)
>320	0.94 (0.03)	0.71 (0.08)	0.77 (0.07)	0.85 (0.07)	0.31 (0.16)

out the Pacific Northwest exhibit a fluvial (both resident and migratory) life history. Thus, it is important to quantify potential differences in key population-level characteristics (e.g., S) between life history forms, which may reveal the need for diverse management actions within a single recovery unit.

Using otolith age estimation, we found bull trout to be relatively long lived in the SFWWR (>9 years), and this age structure is similar to that of adfluvial populations (Fraley and Shepard 1989; Mogen and Kaeding 2005). In contrast, bull trout in the SFWWR achieved sexual maturity at much-smaller sizes (200 mm) and much-earlier ages (3–5 years) than have been reported for adfluvial populations (>480 mm: Baxter and Westover 2000; 6–9 years: Johnston et al. 2007). Differences in size and age at sexual maturity between adfluvial and riverine bull trout may be even more pronounced for strictly resident fish, which can achieve sexual maturity at approximately 150 mm (Hemmingsen et al. 2001). In the SFWWR, we were unable to differentiate between strictly resident and migratory bull trout based on fecundity data (e.g., Downs et al. 2006; but see Homel 2007), and large differences in size at sexual maturity and growth rate may occur between life history types. In addition, there may be considerable variability in the proportion of fish that has achieved sexual maturity within any given size-class or age-group (Hutchings 1996; Hutchings and Jones 1998; Swenson et al. 2007). Ultimately, further work evaluating the differences and variability in age and size at maturity may be important for understanding bull trout population dynamics, the relative contributions of different life history forms to overall population growth, and appropriate management strategies (Johnston et al. 2007).

Age- and stage-specific estimates of S are critical for identifying the life stages that potentially limit a population and its future viability (Williams et al. 2002). Our research is unique in that we used a combination of active and passive sampling techniques to quantify the first published estimates of S for multiple size-classes, age-classes, and life history forms of a fluvial bull trout population. We found considerable variability in annual S among size-classes, but no evidence of size-class × time interaction effects; these data suggest that the relative differences in bull trout S among size-classes were consistent through time. Our results indicate that large, stream-level disturbances affect bull trout S independent of size-class. For example, while there was little variability in maximum and minimum temperatures in the SFWWR during our study, the amount of precipitation was variable across years and 2004 was characterized as having higher-than-average precipitation (study period

average = 114.9 cm, SE = 9; 2004 average = 136.5 cm; U.S. Department of Agriculture, High Ridge Snow Telemetry Station, unpublished data). The higher river flows and velocities associated with the wet year of 2004 may have resulted in lower S for bull trout, which typically use slow-water habitats (Thurow 1997; Muhlfeld and Marotz 2005; Al-Chokhachy and Budy 2007). Ultimately, the mechanism linking these large-scale environmental patterns and bull trout S is unclear; however, our results do indicate the influence of large-scale processes on population-level vital rates independent of size-class.

We were unable to directly compare our estimates of bull trout S with estimates from conspecific populations due to the overall lack of field estimates of S, particularly for different size-classes, age-classes, and life history forms. However, S-values for juvenile bull trout (120–170 mm) in the present study were similar, albeit slightly lower, than those observed for fluvial brook trout juveniles in the northeastern United States (apparent $S = 0.218$, SE = 0.15; Petty et al. 2005), whereas S for bull trout larger than 170 mm appeared to be similar to those of other inland, stream-dwelling salmonids (range of apparent $S = 0.42–0.54$; Budy et al. 2007b). We observed little variability in the annual S of adult bull trout (>170 mm), which indicates that once a bull trout reaches this particular size threshold there is little variation in the sources and rates of mortality. Despite our inability to compare our field estimates with those describing other bull trout populations, the inherent differences in age and size at maturity, migration pattern (e.g., Muhlfeld and Marotz 2005), and subadult rearing (e.g., lacustrine versus riverine), among other factors, suggest the presence of substantial differences in vital rates between life history forms.

Bull trout that exhibited large movements (i.e., moved below WW1) demonstrated substantially higher S than did fish that remained upstream of WW1. These results are contradictory to previously reported patterns of migratory bull trout distribution (Rieman et al. 1997) and abundance (Nelson et al. 2002). In the SFWWR, this higher S may be the result of multiple factors, including greater growth and metabolic rates in warmer downstream reaches (e.g., Thurow 1987) or a reduction in intraspecific competition with the longitudinal decrease in bull trout density (e.g., Paul et al. 2000; but see Johnston et al. 2007). Despite the higher S for fish exhibiting migratory behavior, the link between S and movement below WW1 is unclear due to the high variability in full trout movement patterns (Muhlfeld and Marotz 2005). In the Walla Walla River, habitat conditions are highly degraded due to a diversion structure (~20 km below WW1) that removes a

substantial amount of water from the river; water temperatures below this structure exceed 25°C, habitat is greatly simplified, and flows are reduced to minimal levels (~0.71 m³/s) during summer. Nevertheless, longer movements (>20 km) to these degraded sections by bull trout tagged in the SFWWR study site have been observed in radiotelemetry studies (Mahoney 2002) and through detections during 2005 at a recently installed additional antenna (21 km below WW1). The condition of downstream degraded reaches suggests that bull trout exhibiting these longer migrations could experience relatively high mortality rates.

Despite the high level of habitat quality in the SFWWR above WW1, environmental disturbances within the low-elevation Blue Mountain systems may result in generally lower S for fish remaining in the headwaters. In particular, the relatively high gradient and the potential for flashy, high-flow events (e.g., rain on snow) could result in lower S for fish exhibiting a more-resident life history; low abundance of resident bull trout in Mill Creek, a tributary of the Walla Walla River (Sankovich et al. 2003), is consistent with this idea. Furthermore, some bull trout populations in Oregon are considered to be devoid of resident fish (J. Dunham, U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, personal communication); this suggests that the S of resident fish results from different landscape-level attributes (e.g., Dunham and Rieman 1999).

We used C as a surrogate for fish health (Murphy et al. 1991) and found that this factor accounted for a substantial amount of variability in bull trout S in the SFWWR. The C of an individual can be affected by a number of different biotic (e.g., food availability) and abiotic (e.g., water temperature) factors. In our study, C only accounted for a significant amount of variability in the S of juveniles (120–170 mm), indicating a link between factors that affect the C (e.g., competition for resources; Paul et al. 2000) and ultimately the S of juveniles. On the contrary, the lack of improvement in model fit with C for fish larger than 170 mm suggests that once a fish has obtained a particular length, S is unaffected by C. In the SFWWR, this ontogenetic change may result from different physiological abilities (e.g., swimming ability), changes in foraging opportunities as fish shift to increased piscivory on juvenile resident and anadromous salmonids (Rieman and McIntyre 1993; Clarke et al. 2005), or simply the escape from cannibalism risk upon achieving a larger size (e.g., Beauchamp and Van Tassell 2001). However, in systems that are depauperate in juvenile forage fishes, particularly where native populations of anadromous and resident salmonids have been extirpated or have largely declined or where water temperatures are above 16°C, individual C may have a greater effect on the S of larger bull trout.

Limitations of mark–recapture analyses.—We acknowledge there may be limitations with our mark–recapture analyses of bull trout S. Particularly, we were not able to perform formal goodness-of-fit evaluations, which can affect the overall rank of models (i.e., AIC_c values) and provide insight into violations of model assumptions or structure (Cooch and White 2005). In our analyses, the consistent structure among our top models (total $W_i = 96.7\%$), where S varied by group and time (as an additive term), suggests that changing the AIC_c scores through adjustment in the over-dispersion parameter (Cooch and White 2005) would not have altered the general model structure of our results. However, we acknowledge that overdispersion would result in higher variance in bull trout S estimates (i.e., precision) but would not affect our point estimates (Cooch and White 2005).

We found tag loss to be minimal in this study, but there is some indication of size bias in our capture methods. This difference between the number of bull trout captured and the number observed during snorkel surveys may be the result of low juvenile detection efficiency during snorkeling (Thurow et al. 2006). In addition, we were unable to evaluate for violations of the assumption of homogeneous capture probabilities, but such violations generally lead to only a small negative bias in estimates of S (Williams et al. 2002). Next, we used a multiage mark–recapture model in which fish transitioned from one size-class to the next based on average growth. With this approach, variability in annual growth could have caused some reduction in the precision of S estimates for bull trout larger than 170 mm (Williams et al. 2002) and limited our power to detect significant differences in S of these groups. Despite the potential limitations, our ability to incorporate field estimates of age and growth into our analyses of S, our use of multiple sampling methods and year-round capture–recapture data, and the high sampling effort and sample size should have minimized the bias in our results (Barker 1992; Manly et al. 1999; Williams et al. 2002).

Finally, we acknowledge that the length of our study may not have been conducive to obtaining robust estimates of F and F', and we urge caution in direct interpretation of these results. In particular, long-lived species like the bull trout may exhibit relatively long temporary migrations (i.e., rearing in downstream habitats), and robust estimates of these large-scale movements may require studies of considerably longer duration. However, the uncertainty in these parameters generally has little effect on estimates of S produced by

the Barker model (M. Conner, Utah State University, personal communication).

Population Structure

Bull trout are known to exhibit multiple life history forms within a population, but the contribution of different size-classes within each life history form to overall population abundance is largely unknown. We found that individuals from all size-classes greater than 120 mm exhibited migratory behavior, and the majority of movement was exhibited by fish larger than 420 mm. Our movement results differ from early research, which suggested that bull trout larger than 300 mm were migratory in fluvial populations (e.g., Rieman and McIntyre 1993). We found that only 46% of bull trout greater than 320 mm exhibited migratory behavior (i.e., movements > 12 km from the lower limit of the core spawning area); however, a large percentage (72%) of bull trout larger than 420 mm did exhibit increased migratory behavior. These results could change over time, however, as fish that appear to be resident in behavior may express migratory patterns in subsequent years. Similar to other fluvial (Nelson et al. 2002) and adfluvial (Fraley and Shepard 1989; Downs et al. 2006) populations, SFWWR bull trout exhibited considerable variability in age and size at migration. Overall, managers considering plans for habitat restoration and flow regulation within migratory corridors should incorporate habitat requirements for both juvenile and adult bull trout (Homel and Budy 2008).

We acknowledge that there may be some uncertainty associated with our assessment of bull trout population structure in the SFWWR. This uncertainty is largely due to detection efficiency at the WW1 antenna (Zydlewski et al. 2006). Although our efficiency estimate (50%) was similar to that reported for small streams (e.g., 40–60%; S. Anglea, Biomark, Inc., Boise, Idaho, personal communication), seasonal differences in efficiency could have resulted in underestimation of the migratory fish contribution to the overall SFWWR population (i.e., low detection efficiency during peak migration periods; Homel 2007). However, previous analyses by Homel (2007) did not indicate any seasonal pattern of potential bias due to low detection efficiency or power outages across years.

Conclusions

Our research focused on assessing general patterns of population demographics, structure, and vital rates in a relatively large population of fluvial bull trout. With this, we have provided the first comprehensive field estimates of population structure in a fluvial population containing multiple life history forms and the first estimates of S for different life stages and life history forms. The information available for adfluvial and fluvial bull trout populations suggests that distinct differences (e.g., size at sexual maturity, growth) exist between life history forms (but see Homel 2007) and that different management, restoration, and recovery plans are necessary for bull trout populations composed of these different forms. Our results provide managers with critical information for evaluating the viability of bull trout populations and a template for analyzing the effects of various management and restoration strategies for this imperiled species.

References

Al-Chokhachy, R., P. Budy, and H. Schaller. 2005. Understanding the significance of redd counts: a comparison between two methods for estimating the abundance of and monitoring bull trout populations. North American Journal of Fisheries Management 25:1505–1512.

Al-Chokhachy, R. 2006. Identifying the limiting factors and trends of bull trout (*Salvelinus confluentus*) populations in eastern Oregon. Doctoral dissertation. Utah State University, Logan.

Al-Chokhachy, R., and P. Budy. 2007. Summer microhabitat use of fluvial bull trout in eastern Oregon streams. North American Journal of Fisheries Management 27:1068–1081.

Barker, R. 1992. Effect of heterogeneous survival on bird-banding model confidence interval coverage rates. Journal of Wildlife Management 56:111–116.

Barker, R. J. 1999. Joint analysis of mark recapture, resighting and ring-recovery data with age-dependence and marking-effect. Bird Study 46:82–90.

Baxter, J. S., and W. T. Westover. 2000. An overview of the Wigwam River bull trout program (1995–1999): habitat conservation trust fund final report. Baxter Environmental, Fisheries Project Report KO 58, Nelson, British Columbia, Canada.

Beauchamp, D. A., and J. J. Van Tassell. 2001. Modeling seasonal trophic interactions of adfluvial bull trout in

Lake Billy Chinook, Oregon. Transactions of the American Fisheries Society 130:204–216.

Budy, P., R. Al-Chokhachy, and G. P. Thiede. 2003. Bull trout population assessment and life-history characteristics in association with habitat quality and land use in the Walla Walla River basin: a template for recovery planning. Annual report to the U.S. Fish and Wildlife Service, RWO-38. Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan.

Budy, P., R. Al-Chokhachy, K. Homel, and G. P. Thiede. 2005. Bull trout population assessment in northeastern Oregon: a template for recovery planning. Annual report to the U.S. Fish and Wildlife Service, RWO-38. Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan.

Budy, P., R. Al-Chokhachy, and G. P. Thiede. 2007a. Bull trout population assessment in northeastern Oregon: a template for recovery planning. Annual Progress Report to the U.S. Fish and Wildlife Service, RWO-38. Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan.

Budy, P., G. P. Thiede, and P. McHugh. 2007b. A quantification of the vital rates, abundance, and status of a critical population of endemic cutthroat trout. North American Journal of Fisheries Management 2:593–604.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Clarke, L. R., D. T. Vidergar, and D. H. Bennett. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. Ecology of Freshwater Fish 14:267–277.

Contor, C., A. Sexton, J. Volkman, B. Mahoney, T. Hansen, E. Hoverson, P. Kissner, C. Crump, S. Narum, A. Talbot, and M. Powell. 2003. Walla Walla basin natural production monitoring and evaluation report. Bonneville Power Administration Project 2000-03900, Portland, Oregon.

Cooch, E., and G. White. 2005. Program MARK: a gentle introduction, 4th edition. Available: www.phidot.org/software/mark/docs/book. (November 2007).

Colyer, W. T., J. L. Kershner, and R. H. Hildebrand. 2005. Movements of fluvial Bonneville cutthroat trout in the Thomas Fork of the Bear River, Idaho-Wyoming. North American Journal of Fisheries Management 25:954–963.

Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4:437–445.

Downs, C. C., D. Horan, E. Morgan-Harris, and R. Jakubowski. 2006. Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. North American Journal of Fisheries Management 26:190–2000.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometric landscape characteristics. Ecological Applications 9:642–655.

Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology, and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63:133–143.

Franklin, A. B., D. R. Anderson, R. J. Gutierrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

Hemmingsen, A. R., S. L. Gunckel, and P. J. Howell. 2001. Bull trout life history, genetics, habitat needs, and limiting factors in central and northeast Oregon. Bonneville Power Administration, Project 1994–05400, Portland, Oregon.

Hilderbrand, R. H. 2003. The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. Biological Conservation 110:257–266.

Homel, K. 2007. Evaluating genetic population structure and movement patterns of bull trout (*Salvelinus confluentus*) in northeast Oregon. Master's thesis. Utah State University, Logan.

Homel, K., and P. Budy. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout in northeastern Oregon. Transactions of the American Fisheries Society 137:869–880.

Hutchings, J. A. 1996. Adaptive phenotypic plasticity in brook trout, *Salvelinus confluentus*, life histories. Ecoscience 3:25–32.

Hutchings, J. A., and E. B. Jones. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 55:22–47.

Legault, C. M. 2005. Population viability analysis of Atlantic salmon in Maine, USA. Transactions of the American Fisheries Society 134:549–562.

Johnston, F. D., J. R. Post, C. J. Mushens, J. D. Stelfox, A. J. Paul, and B. Lajeunesse. 2007. The demography of recovery of an overexploited bull trout, Salvelinus confluentus, population. Canadian Journal of Fisheries and Aquatic Sciences 64:113–126.

Leary, R. F., F. W. Allendorf, and S. H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath River drainages. Conservation Biology 7:856–865.

Mahoney, B. 2002. Walla Walla basin summer steelhead and bull trout radio telemetry project. Bonneville Power Administration, Portland, Oregon.

Manly, B. F., L. L. McDonald, and T. L. McDonald. 1999. The robustness of mark–recapture methods: a case study for northern spotted owl. Journal of Agricultural, Biological, and Environmental Statistics 4:78–101.

Marschall, E., and L. B. Crowder. 1996. Assessing population responses to multiple anthropogenic effects: a case study with brook trout. Ecological Applications 6:152–167.

Mogen, J. T., and L. R. Kaeding. 2005. Identification and characterization of migratory and nonmigratory bull trout populations in the St. Mary River drainage, Montana. Transactions of the American Fisheries Society 134:841–852.

Muhlfeld, C. C., and B. Marotz. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. North American Journal of Fisheries Management 25:797–810.

Murphy, B. R., D. W. Willis, and T. A. Springer. 1991. The relative weight index in fisheries management: status and needs. Fisheries 16(2):30–38.

Nelson, M. L., T. E. McMahon, and R. F. Thurow. 2002. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. Environmental Biology of Fishes 64:321–332.

Petty, J. T., P. J. Lamothe, and P. M. Mazik. 2005. Spatial and seasonal dynamics of brook trout populations inhabiting a central Appalachian watershed. Transactions of the American Fisheries Society 134:572–587.

Paul, A. J., J. R. Post, G. L. Sterling, and C. Hunt. 2000. Density-dependent intercohort interactions and recruitment dynamics: models and a bull trout (*Salvelinus confluentus*) time series. Canadian Journal of Fisheries and Aquatic Sciences 57:1220–1231.

Quinn, T. J., II, and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service General Technical Report INT-302.

Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285–296.

Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and the likely future trends of bull trout within the Columbia River and Klamath River basins. North American Journal of Fisheries Management 17:1111–1125.

Ripley, T., G. Scrimgeour, and M. S. Boyce. 2005. Bull trout (*Salvelinus confluentus*) occurrence and abundance influenced by cumulative industrial developments in a Canadian boreal forest watershed. Canadian Journal of Fisheries and Aquatic Sciences 62:2431–2442.

Sankovich, P. M., S. J. Starcevich, A. R. Hemmingsen, S. L. Gunckel, and P. J. Howell. 2003. Migratory patterns, structure, abundance, and status of bull trout populations from subbasins in the Columbia Plateau and Blue Mountain Provinces. Bonneville Power Administration, Project 199405400, Portland, Oregon.

Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Transactions of the American Fisheries Society 130:1026–1037.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262–278.

Swenson, E. A., A. E. Rosenberger, and P. J. Howell. 2007. Validation of endoscopy for determination of maturity in small salmonids and sex of mature individuals. Transactions of the American Fisheries Society 136:994–998.

Thurow, R. 1987. Evaluation of the South Fork Salmon River steelhead trout fishery restoration program. Idaho Department of Fish and Game, Lower Snake River Fish and Wildlife Compensation Plan, Contract 14-16-0001-86505, Boise.

Thurow, R. F. 1997. Habitat utilization and diel behavior of juvenile bull trout (*Salvelinus confluentus*) at the onset of winter. Ecology of Freshwater Fish 6:1–7.

Thurow, R. F., J. T. Peterson, and J. W. Guzevich. 2006. Utility and validation of day and night snorkel counts for estimating bull trout abundance in first- to third-order streams. North American Journal of Fisheries Management 26:217–232.

Tyron, W. W. 2001. Evaluating statistical difference, equivalence, and indeterminacy using inferential confidence intervals: an integrated alternative method of conducting null hypothesis statistical tests. Psychological Methods 4:371–386.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, California.

Wilson, P. H. 2003. Using population projection matrices to evaluate recovery strategies for Snake River spring and summer Chinook salmon. Conservation Biology 17:782–794.

Zydlewski, G. B., G. Horton, T. Dubreuil, B. Letcher, S. Casey, and J. Zydlewski. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. Fisheries 31:492–502.

Appendix: Bull Trout Recapture Data

TABLE A.1.—Number of tagged bull trout that were recaptured from six size-classes (total length) in the South Fork Walla Walla River, Oregon, 2002–2006. Recaptures are reported for each year (summer field sampling) and interval (the period between annual sampling events). Recapture totals account for average annual growth, which was determined from field estimates and figured into the number of recaptures in the next field season.

Size-class (mm)	Interval 2002–2003	Summer 2003	Interval 2003–2004	Summer 2004	Interval 2004–2005	Summer 2005	Interval 2005–2006	Summer 2006	Interval 2006–2007
120–170	5	[a]	28	[a]	34	[a]	17	[a]	14
171–220	3	3	19	8	13	3	9	5	13
221–270	1	0	5	6	8	4	6	7	8
271–320	0	4	2	4	6	12	6	6	3
321–370	3	5	5	3	2	4	4	15	14
371–420	2	4	13	1	6	5	7	6	7
>420	11	12	30	26	28	15	12	24	19

[a] None of the 120–170-mm fish were available for recapture, as all of them entered the 170–220-mm size class.