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ARTICLE

Population Changes after 14 Years of Harvest Closure on a Migratory Population of Bull Trout in Idaho

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Abstract
Primary data (size and age structure, abundance) and derived data (growth, mortality, recruitment) were used to assess the status and trends of Bull Trout *Salvelinus confluentus* in the North Fork of the Clearwater River, Idaho, under a 14-year harvest closure. From 2000 (6 years after harvest closure) to 2008, an increase in the number of larger and older migratory Bull Trout occurred, as evidenced by the rightward shift in the cumulative length-frequency distribution, increases in mean total length and weight, and increases in age. The stability in growth rates over an 8-year interval indicated that the increases in size structure were age related (e.g., recruitment and mortality changes) rather than growth related. The abundance of migratory spawning adults also steadily increased over the period 1994–2008, as indicated by the increases in redd counts. A logistic model fitted to population estimates (not including unsampled portions of the drainage where migratory Bull Trout are known to exist) indicated that the rate of population growth as of 2005 was beginning to slow and that a carrying capacity of 5,215 total migratory adults will be asymptotically approached, surpassing the U.S. Fish and Wildlife Service's drainage-wide recovery goal of 5,000 total adults. The results from an age-structured population model (model 1) indicated a carrying capacity (5,716 migratory adults) similar to that of the logistic model. If the results under model 1 are achieved, the migratory adult population (including nonspawning adults) will surpass 5,000 adults in 2019. The results under a second model depicted a lower carrying capacity (3,592 fish). This analytical approach has promise for application in situations where harvest restrictions or the elimination of fishing are part of Bull Trout restoration programs.

Effective management of a fishery requires adequate understanding of the life histories and vital statistics of the fish stocks. The necessary vital statistics may include size and age structure, abundance, growth, mortality (natural and fishing), recruitment, fecundity, age of maturation, and spawning frequency. With knowledge of such vital statistics and their trends, the effects of management regulations such as harvest curtailment or closure can be effectively modeled and examined, and the effects of alternative management options can be explored (Hilborn and Walters 1992).

One question of interest to many harvest managers is how a population will respond to a curtailment or cessation of harvest, either through no-harvest regulations such as catch and release (Jensen et al. 2009) or temporary or permanent no-fishing or no-harvest regulations, as might occur in closed areas or reserves (Bohnsack 2000; Pillans et al. 2003; Bartholomew and Bohnsack 2005). An increase in the number of larger, older fish should typically be observed as a response to justify the restrictive regulations. If no such increase occurs, some other compensating factor such as high natural mortality rates

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(Barnhart 1989) or habitat limitations (Hunt 1971) may be preventing the potential benefits of the tightened regulations from having the desired result.

Status assessments based on knowledge of key vital statistics are especially important for threatened species such as Bull Trout *Salvelinus confluentus*. In Idaho, a harvest closure was implemented for Bull Trout in the North Fork of the Clearwater River in September, 1994 (which preceded a statewide closure in 1995; Schriever et al. 2004). Bull Trout are considered vulnerable to overexploitation because they grow slowly and produce few eggs relative to other salmonids (Paul 2000; Paul et al. 2003; Post et al. 2003). In 2000, after several years under the closure, studies of migratory Bull Trout life history and temporal and spatial distributions were conducted throughout the North Fork drainage (Schiff 2004; Hanson et al. 2006). Key spawning watersheds, migration corridors, and overwinter areas were described, along with migration timing, behaviors, spawning frequency, adult survival, and the effects of water withdrawals from Dworshak Dam (Hanson et al. 2006). Mean total length of adults, densities in snorkeled reaches, and abundance of spawners based on redd counts were also monitored. Increases in total lengths of individual fish and apparent increasing trends in densities (from snorkel surveys) and redd counts led to the suggestion that the harvest closure had resulted in a positive response by the population (Hanson et al. 2006). It was also suggested that some of the U.S. Fish and Wildlife Service (USFWS) recovery goals set for the North Fork Bull Trout stock were being met (Hanson et al. 2006). Twenty local migratory populations have been documented throughout the drainage (local populations defined as groups of fish spawning in distinct tributaries; USFWS 1998), representing an increase over the 11 populations identified at the time of listing, and overall North Fork migratory population abundance was found to be increasing or stable (DuPont and Horner 2008). Other USFWS recovery criteria for the North Fork that were not met in the Idaho Department of Fish and Game (IDFG) report of 2008, however, were those requiring 15 years of increasing or stabilizing population trends and an overall population of 5,000 total adults (both resident and migratory forms) throughout the entire drainage (USFWS 1998).

A closer, more data-intensive assessment of the population's response to the harvest closure and recent trends was needed. Although migration timing, distribution, and overwintering patterns had been well documented (Schiff 2004; Schiff et al. 2004; Hanson et al. 2006), no comparable analysis of the demographic rates of the stock and their trends (increasing, decreasing, or stable) had been conducted to evaluate the effects of the harvest closure.

In assessing the effects of harvest closure, age-structured models are an improvement over simple, whole-population models because fish of different ages exhibit differential growth rates, fecundities, and contributions of biomass to the catch (Haddon 2001). The effective application of age-structured models, however, requires accurate and precise age estimates, well-defined vital statistics, and knowledge of life history traits.

The objectives of this study were to use empirical data from the North Fork Bull Trout population to (1) assess changes in the size structure, age structure, and abundance of the population after 14 years of harvest closure and (2) develop examples of age-structured population models to assess changes since the harvest closure. If the closure has been successful in retaining fish in the population, one would expect to see an increasing abundance and more larger, older fish than prior to the closure (Barnhart 1989; Jensen et al. 2009). Concurrently, reproduction and recruitment should also be expected to at least remain stable. We believed that investigation into the demography of the North Fork Bull Trout population since the harvest closure would be useful in assessing effectiveness of current regulations and in guiding future management decisions. Such an assessment would also be valuable for other stocks and locations where harvest restrictions or the elimination of fishing are part of Bull Trout restoration.

METHODS

To assess Bull Trout stock status in the North Fork of the Clearwater River after 14 years of harvest closure, we selected an approach based on integrated, dynamic age-structured modeling using size, age, growth, fecundity, and abundance information (primary data) from this project and prior projects (Schiff 2004; Schiff et al. 2004; Hanson et al. 2006; Erhardt 2010). Where primary data were unavailable, data from other unrelated projects were used.

Primary Data Sources

Size structure.—Size-structure data were obtained from annual fish sampling over the period 2000–2008. Migratory Bull Trout were sampled by hook and line in the lower portion of the North Fork and slack-water interfaces of Dworshak Reservoir. Each year, sampling was conducted during the spring at locations where the Bull Trout migrants staged prior to and upon initiation of upriver spawning migrations (Schiff 2004; Hanson et al. 2006). All fish were measured for total length (mm) and weight (g).

The size structure of the population (expressed in length) was assessed for trends over the period 2000–2008. Length analysis was conducted for fish $\geq$350 mm TL because that was determined to be the threshold size of adult sexual maturation (Schiff 2004; Erhardt 2010) and fish were fully recruited to the gear at this length (Erhardt 2010).

Cumulative length-frequency distributions were developed for individual years to visualize changes in fish size and to identify strong year-classes. A Kruskal–Wallis test was utilized to test whether the mean ranked lengths of Bull Trout were different among years. Multiple comparisons were conducted on the ranked data using the general linear model (GLM) procedure (SAS Institute 1998) and performing an analysis of variance. Differences among mean ranks were assessed using Tukey's multiple-range test. A stable length structure was concluded to exist if no significant differences in the length distributions were found. If significant differences were found, linear regression was used to determine the direction of change (increasing or decreasing). An increase in size structure was identified if the slope of the regression applied to the mean ranked lengths was significantly greater than zero ($\alpha = 0.05$).

Age structure.—Fish ages were determined via pelvic fin rays, as collected near the base (proximal end) of the ray from all fish sampled in spring 2003–2005 and 2007–2008. Transverse cross-sections of the rays were made with a Buehler Isomet low speed saw and examined under a compound microscope at 40× magnification. A double-blind protocol was used to estimate ages. Two experienced readers independently assigned ages to sectioned fin rays. If there were no differences between readers, the assigned age was used for the final age assignment. If there were differences between ages assigned, each reader independently re-aged the sample. If differences still existed, both readers examined the structure together and assigned a final age by consensus. Ages were assigned to 405 Bull Trout collected over the periods 2003–2005 and 2007–2008. A detailed assessment of the precision of age determination using a subset of this data was reported in Erhardt and Scarnecchia (2013).

The age structure of the population was characterized as an additional indicator of stock status and to provide a starting point for the age-structured population model. Assessment of age structure is necessary to determine if changes in length are a result of changes in age, growth, or both. For example, an increasing size structure (shift to longer individuals) and constant mean length at age throughout the years would indicate an accumulation of larger, older fish.

Age-length keys were used to assign ages to the fish in each sampling year that were not aged with pelvic rays (for 2003–2005 and 2007–2008). Differences in the mean length at age among years were tested using analysis of covariance. Pairwise comparisons were made between consecutive years, and a Bonferroni correction was applied to maintain the experiment-wise error rate. Growth rates were concluded to be different if the slopes of the *y*-on-*x* regressions of the mean length on age were significantly different (i.e., the age-year interaction term) among years. If growth rates were found to be similar, then ages from 2005 and 2007 were used to develop age-length keys for 2006 and ages from 2003 were used to develop age-length keys for 2000–2002.

Abundance.—Redd surveys were conducted from mid-September to early October 1994–2008 in selected streams within the North Fork drainage by experienced personnel (Hanson et al. 2006; DuPont and Horner 2008). Redd counts were conducted beginning in 1994 in six reaches (one reach per stream). Due to increased knowledge of the Bull Trout spawning distribution from a telemetry study (Schiff 2004), six additional reaches were annually surveyed beginning in 2001 (within five new streams) and three additional reaches were annually surveyed beginning in 2002 (within three new streams), for a total of 15 reaches by 2002. All redd count surveys were conducted in an upriver manner.

Regressions of log-transformed redd counts over time were utilized to determine whether the adult spawning populations within the selected stream reaches were increasing, decreasing, or stable since the 1994 harvest closure (Maxell 1999). Due to the variability in number of reaches completed throughout the years, only reaches that were surveyed for all years were used for analysis. A nonstable population was identified if the slope of the regression of observed redds on year (the intrinsic rate of growth, r) was significantly different from 0 ($\alpha = 0.05$). A nonlinear regression of the logistic model was also fitted to the data to determine the carrying capacity of redds (K_{redd}) in the select streams and the logistic intrinsic rate of growth (r_L). Model fitting was conducted using conditional least square methods (SAS Institute 1998). This method was used because of the observational errors commonly associated with redd count data (Dunham et al. 2001). The logistic growth model takes the form

$$Nr_t = \frac{K_{\text{redd}}}{1 + \left(\frac{K_{\text{redd}} - Nr_{t-1}}{Nr_{t-1}}\right) e^{-r_L}}, \tag{1}$$

where Nr_t is the number of redds at time t.

Derived Data Sources

Primary data sources (size, age, and redd abundance) were used to derive important information on recruitment and adult carrying capacity needed to effectively model the population.

Growth.—Growth of the North Fork Bull Trout population has been described in Erhardt and Scarnecchia (2013), however, in this study we fit growth models to assess growth differences among years. The von Bertalanffy (LVB) growth curve was fitted to the age–length data using nonlinear least-squares methods. The model takes the form

$$L(t) = L_\infty \left[1 - e^{-k(t-t_0)}\right], \tag{2}$$

where $L(t)$ is the length at age t, L_∞ represents an asymptotic length, k a growth coefficient, and t_0 a hypothetical length at age 0. The LVB models were fitted to all years pooled and individual years using similar t_0 parameters. An analysis of the residual sum of squares was used to test for differences in growth curves among years, with the null hypothesis that all curves were coincident (Chen et al. 1992).

Abundance and carrying capacity.—Redd count data and population estimates (Hanson et al. 2006) were fitted to a logistic model to estimate the adult carrying capacity. The logistic intrinsic growth rate (r_L; equation 1) calculated from the logistic redd count regression was used to represent the rate of growth in redds for six streams and was assumed to represent the growth rate in redds for the portion of the drainage sampled in the population estimate. Additionally, it was assumed that the growth rate of redds (r_L) represented the rate of increase in spawning adults. The population estimate of 1,977 migratory spawning adults in 2004 (Hanson et al. 2006) incorporated the largest survey area (1,471 km) and the most random of surveys, so it was assumed that it was the most accurate of all the estimates. The estimate, however, only incorporated specific drainages where sampling occurred and not the entire drainage (e.g., no sampling in Kelly, Weitas, and Canyon creeks). The predicted number of redds from the regression of the logistic model (equation 1) for 2004 was then divided by the 2004 population estimate to determine a ratio of redds to spawning adults. This ratio was multiplied by the redd carrying capacity (K_{redd} from equation 1) to obtain the adult spawning carrying capacity (K_{sa}). The spawning adult logistic population growth model was then simulated as

$$Nsa_t = \frac{K_{\text{sa}}}{1 + \left(\frac{K_{\text{sa}} - Nsa_{t-1}}{Nsa_{t-1}}\right) e^{-r_L}}, \quad (3)$$

where Nsa_t is the abundance of adult spawners at time t. The abundance of adult spawners and K_{sa} were then divided by a range of spawning frequencies (50–80%; encompassing the Hanson et al. 2006 estimate of 75%) to derive a total adult abundance logistic model and determine the total adult carrying capacity (K). These results were compared with the USFWS recovery goal of 5,000 total adults, which includes all life history forms (resident and migratory) for the entire North Fork drainage.

Age-structured population model.—Primary data (size, age, and abundance) and derived data (growth and recruitment) and selected data from other Bull Trout populations were utilized to develop an age-structured model to assess the impacts of harvest closure on the size and age composition of the migratory portion of the North Fork population. This model only represents the areas where IDFG-derived population estimates were made and does not include the entire drainage or any resident life history forms. It is assumed that the migratory adult abundance estimates for the entire drainage are higher because migratory adult Bull Trout have been documented in Kelly, Weitas, and Canyon creek drainages, where no sampling was conducted (Hanson et al. 2006). Second, the model was used to develop estimates of carrying capacity to compare with those of the logistic model and with the USFWS goal of 5,000 adult fish for the entire drainage and all life history forms.

The baseline model functions were similar to a model developed by Post et al. (2003), which was used to simulate alternative harvest options for a hypothetical Bull Trout population. All parameter estimates are shown in Table 1. Migratory Bull Trout were set to mature at age 5 (100%: ages 4–6 documented by Erhardt 2010), and a 50:50 sex ratio was assumed. The growth of individual age groups was modeled with the LVB model derived in the above analysis.

A fecundity–length relationship has not been derived for migratory Bull Trout within the North Fork drainage. However, Schiff (2004) conducted egg counts on resident Bull Trout in Fish Lake, a high mountain lake within the drainage. These estimates were compiled with egg counts from other studies on migratory Bull Trout in Montana and Canada (Brunson 1952; Heimer 1965; McPhail and Murray 1979; Fraley and Shepard 1989; Parker and Wilhelm 2001) and used to develop a relationship for the North Fork migratory stock. First, a fecundity model was fitted to the egg count data using nonlinear least square methods (Figure 1). The fecundity model was described as

$$f = e\text{TL}^h, \quad (4)$$

where f is the number of eggs per female of size TL and e and h are parameters describing the shape of the curve (Wootton 1998). The relationship used for this model predicted a 500-mm TL adult female would produce 2,316 eggs ($e = 0.0000112$, $h = 3.081$). Next, the fecundity–length relationship (equation 4) was converted to a fecundity–age relationship via the LVB model (Power 2007). Finally, the following population-level fecundity model (Post et al. 2003) was developed:

$$E = \sum_{a=5}^{12} \left[N_a \left(e\text{TL}_a^h \right) \cdot Y \right], \quad (5)$$

TABLE 1. Parameter set for an age-structured population model for migratory Bull Trout in the North Fork of the Clearwater River, Idaho.

Parameter	Value	Source[a]
Adult spawning frequency		
(γ)	0.75	a
von Bertalanffy growth curve: $L(t) = L_\infty[1 - e^{-k(t-t_0)}]$		
L_∞	644.71	b
k	0.22	b
t_0	−0.02	b
Fecudity: $E = \sum_{a=5}^{12}[N_a(e\text{TL}_a^h) \cdot \gamma]$		
e	1.12×10^{-5}	d
h	3.081	d
Mortality: juvenile (age 0–5)	0.200	e
Mortality: adult (age 5–12)	0.277	a, c
Beverton–Holt recruitment: $R = \frac{\alpha E}{1+\beta E}$		
Model 1: α	0.004722	f
Model 1: β	7.73×10^{-7}	f
Model 2: α	0.004722	g
Model 2: β	1.23×10^{-6}	g

[a]Sources are as follows: a = Hanson et al. (2006) (from telemetry data for the North Fork stock); b = this study (age–length data); c = Erhardt (2010); d = parameter estimates were derived from egg counts from various studies (Brunson 1952; Heimer 1965; McPhail and Murray 1979; Fraley and Shepard 1989; Parker and Wilhelm 2001; Schiff 2004) to develop a likely relationship for the North Fork stock; e = juvenile mortality, which was set to 0.2, as reported for Lake Trout in lower Kananaskis Lake (Post et al. 2003); f = model 1 (estimates of recruitment [egg to age 0] for the North Fork population, as derived from the adult carrying capacity [predicted from a logistic regression on adult abundance data] and mortality estimates [from d and e], where adult recruitment was assumed to equal the adult mortality rate at carrying capacity and recruitment from egg to age 0 was then back-calculated, given constant mortality rates for juveniles (0.2) and adults (0.277); g = model 2 (estimates of recruitment [egg to age 0] as calculated in f except that the adult population estimate for 2005 was assumed to be the carrying capacity.

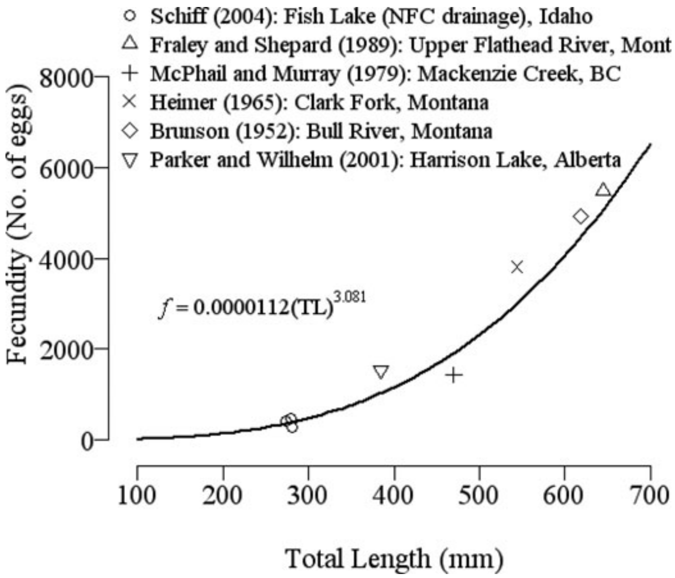

FIGURE 1. Relationship between fecundity (f) and total length derived from the published literature on Bull Trout, which was used to estimate a relationship for the migratory stock of the North Fork of the Clearwater River (NFC) for application to age-structured models.

where E is the number of eggs calculated by summing over all mature spawning females (ages 5–12), e and h are coefficients describing the fecundity of a female of TL_a at age a, N_a is the total number of age-a females, and Y is the percent of females spawning in any given year (i.e., spawning frequency; set as 0.75; Hanson et al. 2006).

Recruitment from total spawning population fecundity to age-0 fish was modeled using the density dependent Beverton–Holt (B–H) stock–recruitment model. Johnston et al. (2007) studied survival of lower Kananaskis Lake Bull Trout and found density dependent survival occurring at early juvenile stages (between egg and age 1) and was followed by constant survival at later ages. This is also consistent with studies conducted on Brown Trout *Salmo trutta* (Mortensen 1977). Johnston et al. (2007) also found the B–H model to be the most parsimonious model (compared to the Ricker (1954) model and density independent models) for describing the density-dependent relationship. The B–H model was parameterized as

$$R = \frac{\alpha E}{1 + \beta E} = \frac{S}{\alpha^* + \beta^* S}, \tag{6}$$

where R = recruits, S = spawners, and the parameters $\alpha^* = 1/\alpha$, $\beta^* = \beta/\alpha$. The maximum number of adults was assumed to be the carrying capacity of the spawning adults (K_{sa}) from the logistic regression analysis (model 1) divided by Y. The number of adult recruits at carrying capacity is then equal to the number of adult mortalities (i.e., births = deaths at carrying capacity). Next, the number of age-0 fish necessary to produce the number of maximum adult recruits was calculated based on the reported per capita natural mortality rate of 0.2 for age-0 to age-5 Lake Trout *Salvelinus namaycush* in Kananaskis Lake (Post et al. 2003). The calculated value was set as the asymptotic recruitment (R_p) of age-0 fish for the relationship where $R_p = 1/\beta^*$. The maximum number of recruits per unit stock as it approaches zero was calculated using methods described by Post et al. (2003). We assumed that if a female is of a size that produced 2,000 eggs (i.e., an age-5 female), then using $\alpha = 0.00472$ resulted in a 3.77 recruits per female at age of first maturity.

The population was also modeled under the assumption that the 2005 population estimate of 1,913 migratory spawning adults (2,550 total adults) was the carrying capacity and the percent of age-5 fish in the sample represented maximum adult recruitment. Model 2, which assumed a lower carrying capacity, was more conservative because redd trends suggest the possibility that the population (and the carrying capacity) has already increased beyond the 2005 adult population estimate. These two models were designed to depict possible future states, which would need to be corroborated with actual data in future years.

In model runs, the age structure of the population was initialized with age estimates from 2005, which had the largest sample sizes of age estimates with the highest accuracy and precision (Erhardt 2010). The population estimate for 2005 (1,913 spawning adults; 2,550 total adults with 75% spawning frequency) came from work conducted by IDFG (Hanson et al. 2006) and was compared with the predicted size from the logistic model. The discrete total annual mortality rate was set as 0.277, as described by Erhardt (2010) and Hanson et al. (2006).

The model was evaluated by generating a predicted age structure based on model inputs and comparing it with the existing age structure data from 2006 to 2008. The model was run until a stable age distribution was reached. At that point, estimated abundance (carrying capacity) was compared with carrying capacity estimates derived from logistic model fits of redd counts and population size data.

RESULTS

Size Structure

An increase in the number of large migratory Bull Trout in the North Fork drainage was evident from 2000 to 2008, indicating a nonstable size structure. The cumulative length-frequency distributions of adult Bull Trout ($\geq$350 mm TL) show an increase in the overall size structure of the population throughout the years (Figure 2). Mean total length of adult Bull Trout captured increased from 416 mm (SD = 43.6) in 2000–468 mm (SD = 66.6) in 2008 with a high of 478 mm (SD = 65.2) in 2007. The mean ranked length was significantly different between at least two years for all samples (Kruskal–Wallis $\chi^2 = 63.56$, df = 8, $P < 0.001$). Results from the regression support the findings of the cumulative length-frequency distributions and indicated an increase in mean length ($F_7 = 25.2$, $P = 0.002$). From 2006 to 2008, however, no significant differences in mean ranked length

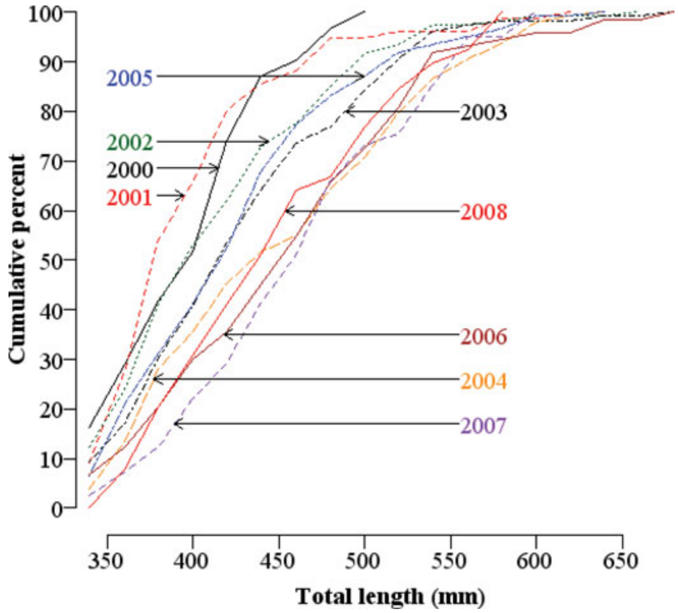

FIGURE 2. Cumulative length-frequency distributions for North Fork migratory Bull Trout ≥350 mm TL captured by hook and line during spring 2000–2008.

were found in the multiple comparisons among the 3 years. This result is what would be expected if stabilization in size structure (i.e., no changes) was beginning to occur.

Age Structure

The results from the age-structure analysis confirm that the increasing size structure of the population was a result of an increase in older individuals in the population. Mean ages of sampled Bull Trout increased from 4.4 years in 2000 to 5.7 years in 2008. Migratory Bull Trout within the North Fork exhibited similar growth rates among years, indicating that the increase in size structure was not related to increased growth but to an increase in age. The only significant difference in growth among years was found between 2004 and 2005 (ANCOVA: $F = 7.27$, $P = 0.008$).

Growth

The LVB model indicated a fast growth rate with an asymptotic maximum size of 645 mm TL. The ages estimated from the 189 pelvic fin rays ranged from 3 to 11 (mean = 5.47, SD = 1.61) and total lengths ranged from 274 to 664 mm (mean = 438.30 mm, SD = 82.43). The pooled LVB model converged on all parameters and was described as $L_t = 644.71(1 - e^{-0.22(t-0.02)})$. The model only converged for the individual years of 2005, 2007, and 2008 and only these years were used for the analysis. The results from the residual sum of squares test among years failed to reject the null hypothesis ($F = 1.06$, $P = 0.39$, df = 6, 180) that all years are coincident, indicating that the LVB growth curves for 2005, 2007, and 2008 were not different.

Abundance

Increases in redd counts were found through the duration of sampling (1994–2008). Bostonia and Placer creeks (within one of the headwaters of the North Fork watershed; Figure 3) were the only streams whose surveys were conducted in all years from 1994 (the first year of no harvest) to 2008. The combined redd count totals ranged from 1 in 1995 to 28 in 2007. In 2008, 16 redds were counted. Combined redd counts in those two streams showed a significant increase with time ($F_{13} = 38.7$, $P < 0.001$, $r^2 = 0.82$). The relationship was described by $\log_e$(number of redds) = 0.21(year) − 420.9. The plot of annual redd counts also suggested the presence of strong adult year-classes at 4-year intervals (Figure 3).

The remaining streams surveyed showed similar increases in redds throughout the study. The highest number of redds observed was in 2007, when 221 redds were counted in 19 reaches. In 2008, there was a decrease to 154 redds observed in 16 reaches. Only four streams were surveyed every year from 1996 to 2008; these counts increased significantly ($\log_e$[redds] = 0.22·year − 441.17; $F_{11} = 54.7$, $P < 0.001$; Figure 4) over the 13-year period.

The logistic model, fit to the redd count data from 1994 to 2008, also indicated an increasing population with a logistic intrinsic growth rate (r_L) of 0.354 ($t = 2.6$, $P = 0.023$). The model also indicated that these six streams will slowly approach a carrying capacity (K_{redd}) of 139 redds ($t = 2.3$, $P = 0.040$). The model projects the six streams to reach 138 redds by 2018, i.e., 24 years after the 1994 implementation of the harvest closure.

The growth rate applied to the migratory adult spawning population estimate for 2004 ($\hat{N} = 1{,}977$ adults) indicated that the population was 112 spawning adults in 1994 and that it will slowly near the maximum carrying capacity (K_{sa}) of 3,911

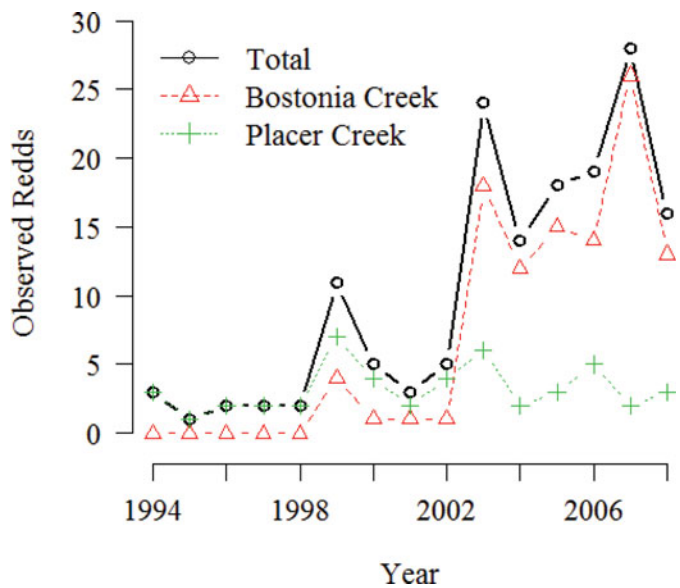

FIGURE 3. Observed Bull Trout redds in two North Fork streams (Bostonia and Placer creeks) from 1994 to 2008.

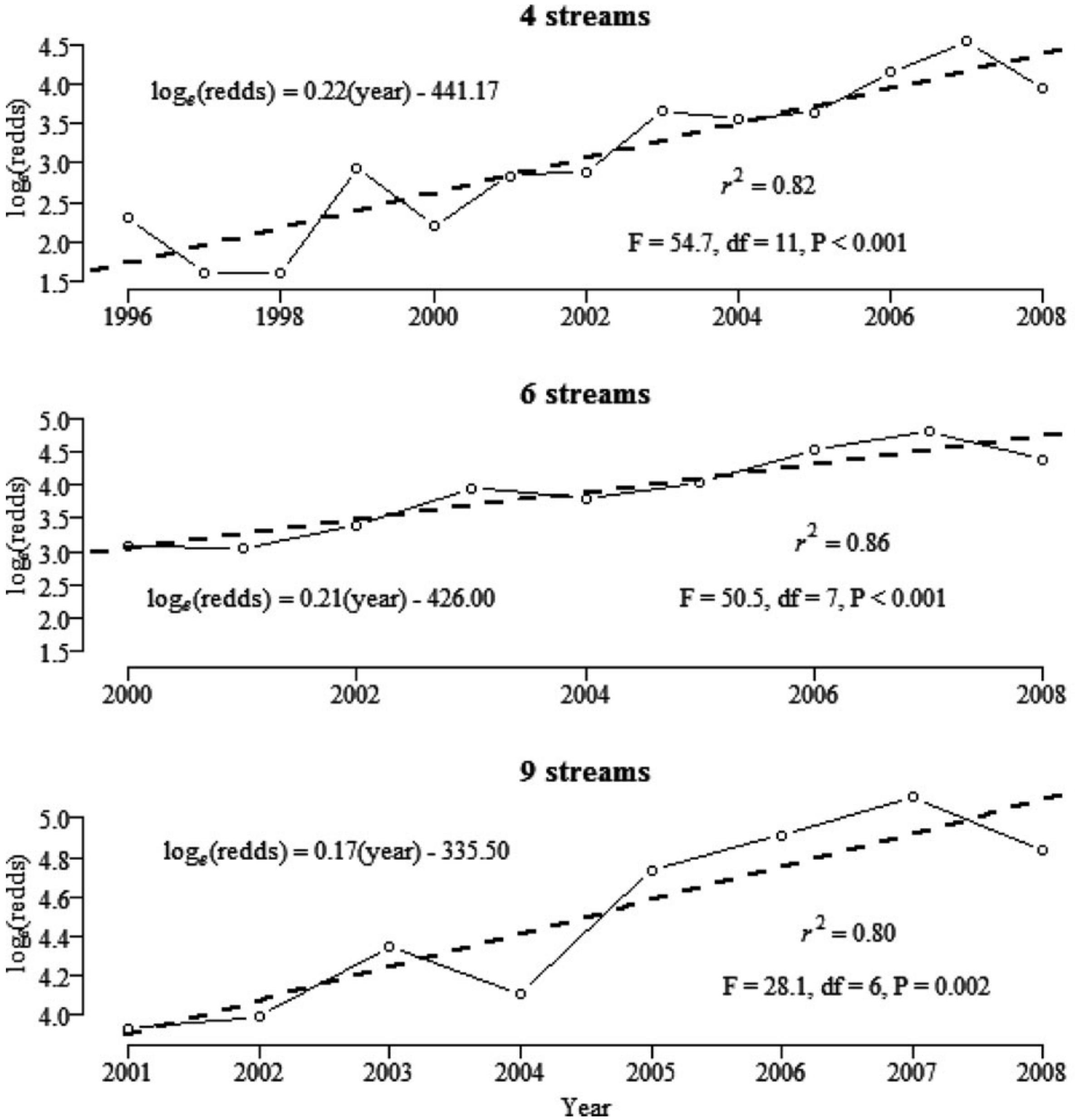

FIGURE 4. Linear regressions of $\log_e$-transformed redd counts of North Fork migratory Bull Trout versus time. The equations were developed for streams in which transects were conducted every year from 1996 to 2008 (four streams), 2000 to 2008 (six streams), and 2001 to 2008 (nine streams).

spawning adults in 2028, or 34 years after the 1994 implementation of the harvest closure. All confidence intervals around the adult spawning population estimates from 2002 to 2005 encompassed the population trajectory. In terms of total adults and present levels of spawning frequency (75–80%) this indicates that the population would surpass the 5,000 level set as a recovery goal by USFWS and reach a total adult carrying capacity (K) of 5,215 (for 75% spawning; Figure 5). Based on trends in redd counts, data fitted to the logistic model indicated that the adult Bull Trout population in the North Fork may thus meet the USFWS recovery goal of 5,000 adults by 2015.

Age-Structured Population Model

The stock–recruitment relationship from egg (E) to age 0 (R) for model 1 was defined by $R = 0.0047E/(1 + 7.73e^{-7}E)$ and for model 2 by $R = 0.0047E/(1 + 1.23e^{-6}E)$. Predicted adult cumulative length frequencies from both models were similar to catch-at-age data from sampling conducted in 2006–2008 and age–length keys developed in the age-structured analysis (Figure 6). Model 1 projections indicated the stock would stabilize (in abundance and age structure) at 5,716 total adults (in 2069), surpassing the USFWS recovery goal of 5,000 fish in 2019. In contrast, model 2 predicted the population would stabilize at

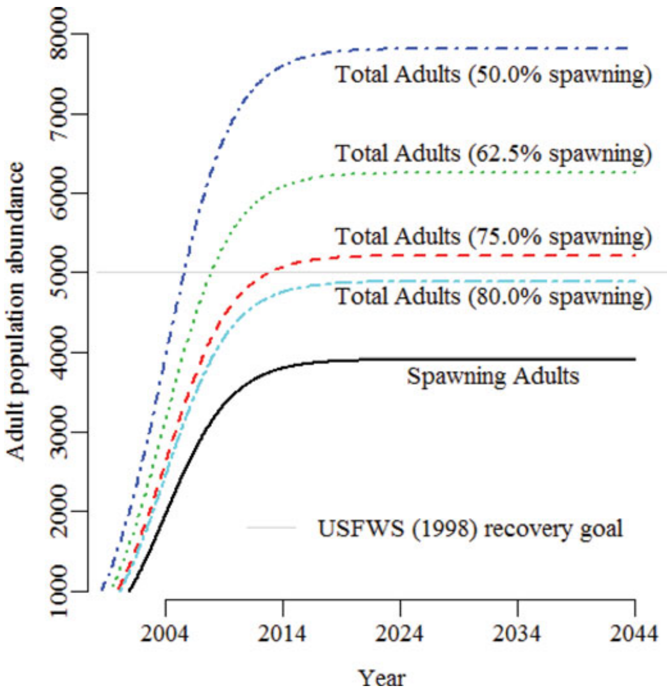

FIGURE 5. Logistic model estimates of the adult population of North Fork migratory Bull Trout compared with the U.S. Fish and Wildlife Service recovery goal of 5,000 adults. The intrinsic rate of growth was derived from redd counts from 1994 to 2008. The population estimate in 2004 was based on estimates from Hanson et al. (2006). Total adult abundances were estimated from the spawning frequency findings (80%) reported by Hanson et al. (2006), and additional frequencies were added for comparison.

3,592 total adults (in 2050). The 5,000-fish recovery goal would only be met if the actual population response to a harvest closure is between models 1 and 2.

DISCUSSION

Status and Trends

The results from the analyses of size and age data indicate that from 2000 (i.e., 6 years after the initiation of a harvest closure) to 2008, an increase in the number of larger and older migratory Bull Trout occurred throughout the North Fork. This conclusion is supported by the right shift in the cumulative length-frequency distribution (Figure 2), the increases in mean length, and increases in age. The stability in growth rates over the 6-year interval indicated that increases in size structure were age-related (e.g., recruitment and mortality changes) rather than growth-related (Neumann and Allen 2007). The last few years of data (2006–2008), however, suggest that the size structure of the population is stabilizing. Additional years of data are needed to verify this. If the population size structure is stabilizing, then the response time (12 years) from harvest closure is equivalent to the lifespan of Bull Trout (Goetz 1989; Erhardt 2010). Näslund et al. (2005) found similar responses with Grayling *Thymallus thymallus* in northern Sweden. Their study found increases in trophy-sized fish for a 10-year period following catch and release implementation; they argued that at least 10 years is needed to fully assess the effects of the restrictive regulations. This time frame is also equivalent to the 10-year lifespan of Grayling (Northcote 1995).

Similarly, the increases in redd counts (Figure 3) indicated that abundance (population size of migratory spawning adults) has steadily increased. The six streams where long-term trend data were available experienced a 31-fold increase in redd counts in 14 years (1994–2007) from a minimum of 4. These results are similar to what Johnston et al. (2007) reported on migratory Bull Trout in lower Kananaskis Lake, Alberta. They reported a 28-fold increase in adult density during a 10-year period after harvest closure from a minimum of 60 individuals. The trend toward larger, older fish may result in further increases in population numbers in the next several years because larger and more fecund fish are beginning to contribute to the reproductive potential of the population.

Most recently (post 2005), the population has been increasing at a slower rate than earlier in the period (pre 2005); no significant increases in the size structure were found over the period 2006–2008. This slowed rate of increase may indicate that the population is moving towards a stable age distribution and its carrying capacity. Redd counts in 2008 (and recent data from 2009) were lower than in 2007. An important question to answer is how much larger the population can become. That is, what is the carrying capacity of the available riverine and reservoir habitat for this migratory population and when would it be reached? Under the assumption that the rate of increase in redd counts ($r = 0.354$) from six streams represents the rate of increase of the migratory adult spawning population, the logistic model projects that the carrying capacity of the total North Fork spawning adult population (for areas only represented in the population estimate) would be 3,911 fish (5,215 total adults with 75% spawning frequency). The total adult population for the entire drainage would therefore be higher because migratory Bull Trout have been documented in drainages not included in this analysis (e.g., Kelly, Weitas, and Canyon creeks). Age-structured model simulations indicate carrying capacities that encompassed this estimate (model 1 = 5,700 fish; model 2 = 3,500 fish). All of these estimates, however, are strongly influenced by model responses to the observed decline of redds in 2008. This decline forces an otherwise strongly increasing population size to level off toward an asymptote in both the logistic model and the B–H stock–recruitment relationship. More years of data at higher stock sizes (i.e., higher redd counts) are needed before the actual range of carrying capacities can be accurately narrowed down. If the current carrying capacity estimate from the logistic fit is accurate, however, and assuming that 75% of adult fish migrate to spawn yearly (based on telemetry research; Hanson et al. 2006) the estimate would exceed the drainage-wide USFWS recovery goal of 5,000 total adults, which includes resident adults, by 215 fish in the year 2015. The observed past ability of the population to increase in size following harvest

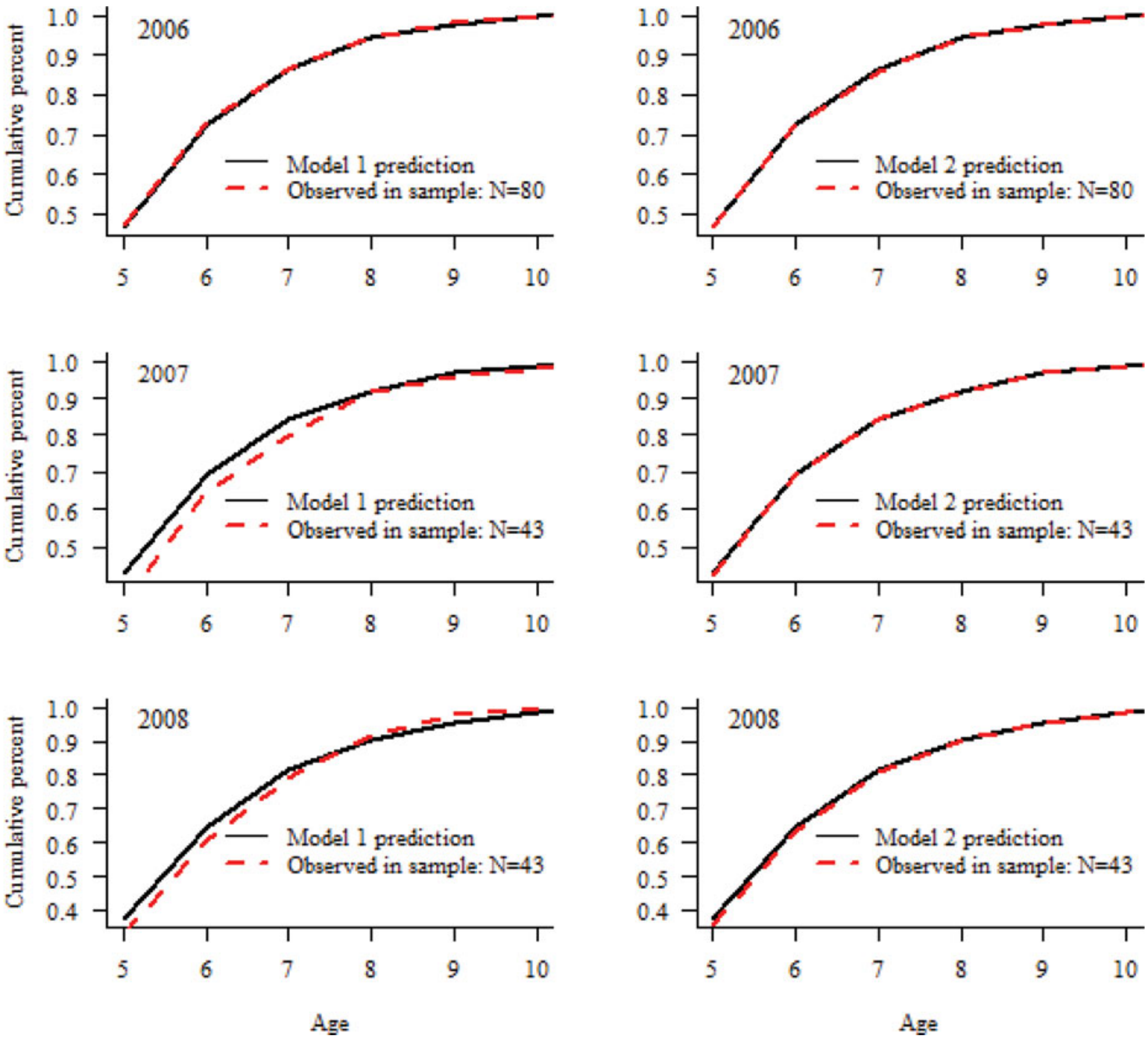

FIGURE 6. Cumulative length-frequency distributions of North Fork migratory Bull Trout predicted by age-structured population models and the observed catch at age from hook-and-line sampling conducted in spring 2006–2008. Model results are derived from simulations representing the maximum adult recruitment based on carrying capacities of 5,215 (from redd count data; model 1) and 2,550 (the population size in 2005; model 2).

closure indicates that the population was large enough to escape depensatory mortality processes or Allee effects, at least in the short term. Such processes can lead to population collapse even after harvest cessation (Frank and Brickman 2000).

The adult spawning estimate (3,911) is above the conservative effective population size (N_e) recommended by Rieman and Allendorf (2001) of 1,000 spawning adult Bull Trout to maintain (in any drainage) adaptive genetic variation. Rieman and Allendorf (2001) also stated that this number could be relaxed if there was clear evidence that the total adult population was larger than the total spawning population.

Data Limitations and Future Needs

The redd count data were used as the basis of model predictions of Bull Trout carrying capacity because it was the longest data set available. The use of redd counts for determining trends, however, has been questioned by various authors (Rieman and McIntyre 1996; Dunham et al. 2001; Al-Chokhachy and Budy 2005). For Bull Trout, this requires several years of data collected by experienced personnel (Howell and Sankovich 2012). The accuracy of redd-count trend data for analysis should be critically examined because it has major impacts on carrying capacity estimates and, hence, recruitment estimates (from egg to age 0) for the age-structured models we tested. For example, doubling the β parameter (from equation 6; $\beta = 3.87 \times 10^{-7}$) in the B–H recruitment model (for model 1) would result in the population stabilizing at 11,000 adults, whereas halving the estimate ($\beta = 1.55 \times 10^{-6}$) would result in a projected carrying capacity of 2,800 adults. Further identification of high-density spawning areas should be evaluated prior to attempting to make adult abundance estimates from the counts; a few index populations may not adequately represent the dynamics of regional populations (Rieman and McIntyre 1996). For example, Downs and Jakubowski (2006) found that on average 3.2

adult Bull Trout entered tributaries of Lake Pend Oreille, Idaho, for every redd that was counted during the annual surveys. Applying this ratio to the 2005 count of 202 redds (in 26 reaches surveyed) suggest that the number of spawning adults would be 646. Using this same ratio, the adult spawning population estimate for 2005 (1,913 fish) would suggest that about 66% of the actual redds were not seen in 2005. Dispersion of adult fish into unsampled streams can present another problem. Hanson et al. (2006) documented several radio-tagged individuals entering tributaries that redd counts have not been consistently conducted on and were not represented in the population estimates, such as the Kelly, Weitas, and Canyon creek drainages. Furthermore, the spatial distribution, which has been well documented for several years, may be increasing slowly as new spawning areas are repatriated by migratory fish and habitat conditions are improved. If redd counts continue to provide the best estimates of stock size in the North Fork, their reliability should be evaluated. A measure of observer error within the drainage should be attempted to develop more precise estimates (Muhlfeld et al. 2006). Redds in additional reaches should be enumerated throughout the Kelly, Weitas, and Canyon creek drainages to increase the percentage of habitat surveyed and move closer to a drainage-wide population estimate.

Age-structured population models for Bull Trout have recently been developed because they allow for specific age and sex demographic rates to be utilized (Rieman and McIntyre 1993; Post et al. 2001; Post et al. 2003). These models, however, typically require much more data than most population studies can provide. Even after years of studies on the North Fork population, data deficiencies remain. Future modeling efforts would benefit from more information on recruitment dynamics (i.e., stock–recruitment relationships), juvenile mortality rates, fecundity relationships, and continued monitoring of fish growth. In our study, juvenile mortality rates and fecundity were estimated from other published studies because no data were available for the North Fork. Although fish we found that growth was not different between a few years at higher stock sizes, the constancy of growth rates for all stock sizes should be assessed because density dependent growth could impact age-structured model results (Lorenzen and Enberg 2002). The largest assumption was the recruitment relationship. More reliable conclusions can be drawn when future monitoring trends verify the carrying capacity as indicated by the logistic model or until stock–recruitment models are better defined and developed. Until then, results from more conservative models (e.g., model 2) are recommended for assessment of the North Fork population.

Modeling in our study was conducted based on the results from a portion of the migratory component of the population. No assessment of resident life history forms were made; such an assessment would be useful in better justifying and refining an appropriate numerical goal for recovery. The relationship between adfluvial and resident life history forms may be influential because these forms can give rise to one another (Rieman and McIntyre 1993). The importance of both forms in the drainage (i.e., increased diversity and genetic exchange; Rieman and Allendorf 2001) is especially important for species inhabiting variable environments (Rieman and McIntyre 1993) and the interaction of the different forms needs further investigation.

Because our study has no controls (i.e., continuously fished areas) but instead relies on trend data (post-harvest closure), adequate future monitoring is critical. Under reestablishment of harvest of any kind, it would be important to closely monitor and obtain information on the population's demographic rates, including harvest mortality, incidental hooking mortality, reproductive success, recruitment, and growth. Although recent trends show an increasing population since the harvest closure, favorable environmental variables may have contributed to the population response. Other salmonid species throughout Idaho have shown increasing trends since 1994 without any major changes to harvest regulations (High et al. 2008). With or without an implementation of harvest, additional years of sampling and monitoring will provide important information regarding population trends of North Fork Bull Trout. The models developed in this study also should be assessed for reliability and predictive capability as new information becomes available. If management of the Bull Trout fishery changes, conservative measures are recommended until more data on demographic rates and trends are available and adequate monitoring programs are in place. Similar data collection and modeling efforts may be useful in other localities to assess effects of harvest regulations on Bull Trout stock status.

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