2018 Deschutes River Fisheries Monitoring Report:

Evaluating sampling designs and the use of boat electrofishing in the assessment of Redband Trout status in the middle and upper Deschutes River

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Abstract

Concern for Redband Trout in the middle and upper Deschutes River led to an evaluation of the feasibility and reliability of three sampling designs to monitor trend in population status. From 2012 through 2014, repeated fish surveys were conducted using boat electrofishing in 43 sites during the irrigation and water storage seasons in the river segment from Big Falls upstream to Wickiup Dam (150 river km). N-mixture and closed capture sampling designs produced low individual detection probabilities and resulted in highly imprecise abundance estimates that were unreliable for tracking trend in status of Redband Trout and sympatric salmonids. The occupancy sampling design produced relatively high species detection probabilities and reliable reach-level estimates of occupancy probability. Sampling during the irrigation season (July through September) showed higher detection probabilities than sampling during the storage season (November through April). Large Redband Trout (>180 mm) showed relatively low occupancy and abundance in reaches 4 and 5 (Spring River to Wickiup Dam). Factors limiting Redband Trout occupancy and abundance in these reaches may include negative interactions with nonnative Brown Trout and hatchery-stocked fish and adverse effects of Wickiup Dam and the managed flow regime. The representativeness of the occupancy study design could be improved with an increase in sampling effort in river sections inaccessible to the boat, which would require additional methods for sampling. If reliable adult abundance estimates are desired, either substantial increase in effort and improved capture methods will be needed using these abundance estimators or more robust sampling designs should be explored.

Introduction

Potamodromous Rainbow Trout (*Oncorhynchus mykiss*) populations in the Columbia River Basin that occur east of the Cascade Mountain range are commonly known as Redband Trout (*O. m. gairdneri*). Redband Trout status and conservation have received recent range-wide attention because many populations have experienced large reductions in distribution due to habitat alteration and fragmentation and negative interactions with introduced nonnative salmonids (Muhlfeld et al. 2015). Although a recent range-wide status assessment found Redband Trout still widely distributed in the western United States, this species has declined an estimated 58% from its historical range (Muhlfeld et al. 2015). Similarly, a century of anthropogenic ecological changes has caused concern about the population status and trend of Redband Trout in the middle and upper Deschutes River in central Oregon.

This section of the Deschutes River was once recognized for the extraordinary steadiness of its intra- and inter-annual flows (Gannett et al. 2003) and as an important recreational trout fishery (Fies et al. 1996). During the past century, humans have altered the flow regime, riverine habitat, and fish assemblage.



Figure 1. Study area map of the Deschutes River in central Oregon.

These changes and their effects include irrigation storage dams that block upstream access to historical spawning grounds (Fies et al. 1996) and restrict downstream transport of sediment and organic matter needed for spawning gravels and habitat complexity (Ligon et al. 1995); water management that reduces food and habitat availability and causes direct fish mortality by stranding fish in dewatered side channels and by instream ice formation (Fies et al. 1996, NPCC 2004); hatchery stocking of Rainbow Trout that may compete or hybridize with native Redband Trout; and the introduction of Brown Trout (Salmo *trutta*), which can have a competitive advantage over other trout species (Fausch and White 1981; Shirvell and Dungey 1983; Wang and White 1994; McHugh and Budy 2005, 2006) and may be favored by the water management regime in the upper Deschutes River (NPCC 2004). These past changes also led to the extirpation of Bull Trout (Salvelinus confluentus) in the 1950s and a perceived decline in Redband Trout abundance (Fies et al. 1996). In the near future, the expected growth in human population (PRC 2015) and demand for water (Newton et al. 2006) in this region could affect Redband Trout habitat in the middle and upper Deschutes River. Water temperature also is projected to increase based on climate warming models (IPCC 2014) and native trout of all species in this region are projected to lose thermally suitable habitat and negative interspecific interactions may be exacerbated (e.g., Wenger et al. 2011). Past ecological alterations, current river management for human use, increasing human pressure on riverine habitat and water quality, and the perceived decline in Redband Trout abundance have led to management concern about the status of this population and highlighted the need for information to accurately assess status and monitor the population response to river management, conservation actions, and climate change.

To obtain a reliable population status assessment, sampling designs that incorporate estimates of detection and evaluate the reliability of the status estimator and feasibility of the sampling method are recommended (Muhlfeld et al. 2015). To address these needs, a field study was designed to obtain baseline information on the current status of native Redband Trout in large river habitat and begin evaluation of monitoring protocols that will enable managers to track fish population trends and guide research and management activities in the middle and upper Deschutes River. Brown Trout and Mountain Whitefish *Prosopium williamsoni* also were captured during the study and were included in the analysis.

The specific objectives were the following:

1) Evaluate the feasibility and reliability of sampling designs to estimate status and monitor trends of Redband Trout populations and sympatric salmonids.

2) Determine current status of Redband Trout and sympatric salmonids.

Study Area

The Deschutes River headwaters emanate from the eastern slope of the Cascade Mountains in central Oregon (Figure 1, inset). This area receives about 254 cm of precipitation each year, mostly as snow. The high elevation forest community of western hemlock *Tsuga heterophylla* and alpine and subalpine plant species transitions in the mid-elevations to a forest community dominated by lodgepole *Pinus contorta* and ponderosa *P. ponderosa* pines. Around the city of Bend, the river enters the Cascade Mountains rain shadow and the semi-arid continental climate of the high desert plateau, which is characterized by the sagebrush steppe plant community (NPCC 2004). Riparian vegetation is dominated by Ponderosa pine and lodgepole pine, willow thickets, and sedge meadows (Fies et al. 1996). Salmonids indigenous to the upper Deschutes River are Redband Trout, Bull Trout (now extirpated), and Mountain Whitefish (Fies et al. 1996). Nonnative salmonids introduced include Brown Trout and Brook Trout *S. fontinalis*. Hatchery Rainbow Trout and Redband Trout strains are stocked annually in the upper Deschutes River basin.



Figure 2. Daily mean discharge of the Deschutes River just downstream of Wickiup Dam, at Benham Falls, and just downstream of North Canal Dam in the city of Bend for the study years: 2012 (thick black line), 2013 (thin black line), 2014 (gray line). Historical mean daily discharge (orange line) and daily minimum and maximum (ribbon) are also shown. At the Wickiup Dam station, historical discharge was estimated using a U.S. Bureau of Reclamation (BOR) hydrological equation for the period from 1983 to 2017. At the Benham Falls and Bend stations, historical discharge was summarized from actual discharge records from 1924 to 1939 (i.e., prior to the construction of Wickiup and Crane Prairie dams). Historical discharge downstream of the city of Bend does not include Tumalo Creek. All hydrograph data were obtained from the BOR Hydromet website (www.usbr.gov/pn/hydromet/).

The study area is commonly described as two segments, the middle and upper Deschutes River (Figure 1), which differ in their fluvial geomorphology and managed discharge regime. The study area was further divided into five sampling reaches delineated by falls, dams, and tributary confluences (Figure 1). These sampling reaches also generally corresponded to genetic structuring, determined after this study occurred (see Bohling et al. 2017), of four major Redband Trout groups: Reaches 1 and 2; Reach 3; Reach 4 (strongly influenced by hatchery introgression); and Reach 5. The middle segment was defined as extending from Big Falls (river kilometer [RK] 213), which is the historical upstream end of anadromous salmonid distribution in this river, to the North Canal Dam (RK 265) in Bend, which until 2017 had no upstream fish passage facilities. Tumalo Creek is the only major tributary in this segment, with annual mean daily discharge of 1.9 m³s⁻¹ and mean daily summer discharge reduced to 0.3-0.6 m³s⁻¹ through diversion for drinking water and irrigation. Other potential barriers to upstream fish movement include Odin Falls (RK 225), Cline Falls (RK 233), Awbrey Falls (RK 246), and the North Canal Dam. Maximum water temperature in this segment ranges from 18-24 °C during the summer and 0-7 °C in the winter. The middle segment is characterized by relatively high reach gradient (mean, 0.7%) and constraining canyon geology. Historical daily mean discharge prior to irrigation development varied annually between 28.3-39.6 m³s⁻¹ (Figure 2, estimated at Benham Falls, U.S. Bureau of Reclamation). In 2014, mean daily discharge was 10.6 m³s⁻¹, with minimum discharge of 2.1 m³s⁻¹ during the irrigation season.

The upper Deschutes River was defined as extending from the North Canal Dam (RK 265) upstream to Wickiup Dam (RK 365). Three major tributaries enter the Deschutes River in this segment: Spring River (annual mean daily discharge, 4.2 m³s⁻¹, RK 306), Little Deschutes River (10.9 m³s⁻¹; RK 311), and Fall River (4.2 m³s⁻¹; RK 330). Maximum water temperature ranges from 10-18°C in summer and 0-7°C in winter. From Bend upstream to the Little Deschutes River confluence the river flows through basalt formations that result in a series of falls and cascades. In this section the river splits into two channels around Lava Island, one of which is dewatered when flows are reduced at Wickiup Dam for reservoir storage. Lava Island Falls (RK 281), Dillon Falls (RK 286), and Benham Falls (RK 291) may be barriers to upstream movement by fish during certain flows. The Deschutes River from North Canal Dam to Benham Falls is relatively high gradient (mean, 0.8%). From the Little Deschutes River upstream to Wickiup Dam, the river is sinuous and low gradient (mean, 0.1%), except at Pringle Falls (RK 349), which may be an upstream passage barrier for fish at low flows. Historical daily mean flows ranged from 14.2-19.8 m³s⁻¹ in winter and 19.8-28.3 m³s⁻¹ in summer where Wickiup Dam was built (Figure 2). Since the 1990s, flows average 4.0 m³s⁻¹, often dropping below 1.4 m³s⁻¹, during the storage season; discharge increases to 38.2 m³s⁻¹ in summer as water is released for irrigation diversion downriver.

		÷		Individual	Sites	All	Sites	Electrofishing Time (min/visit)			
Year	Segment	Season	Per Season (N)	Per Length Mean Season (m) Completion V (N) Period (d)		Median Visits/Site (N)	First Date	Last Date	Mean	Min	Max
2012	Middle	Irrigation	8	200	27	3	Sep 6	Oct 9	6.0	3.0	15.0
		Storage	8	200	6	3	Oct 15	Oct 28	2.5	1.9	3.4
	Upper	Irrigation	11	200	28	3	Sep 3	Oct 3	11.7	2.3	17.3
		Storage	21	200	19	3	Oct 15	Dec 13	9.8	2.9	18.4
2013	Middle	Irrigation	21	100	11	3	Aug 1	Aug 29	1.8	0.9	2.6
		Storage	21	100	7	3	Nov 12	Nov 21	1.6	1.0	2.9
	Upper	Irrigation	21	200	11	4	Aug 5	Oct 3	9.6	1.6	16.5
		Storage	17	200	5	3	Oct 16	Nov 7	6.8	2.2	14.0
2014	Upper	Storage	21	300	15	4	Mar 4	Apr 17	10.0	2.7	16.4
	Middle	Irrigation	20	300	32	4	Jul 1	Jul 30	4.3	2.5	10.5

Table 1. Summary of sampling characteristics by year, segment, and season. Mean completion period refers to the mean number of days from the first to the last date of sampling individual sites in a single season. Electrofishing time is summarized by visit.

Methods

Fish sampling

Within the study area, only river sections that were safe to survey and accessible to the electrofishing boat were considered for sampling. High channel gradient, falls, and a lack of boat access resulted in a discontinuous sampling frame, from which 21 study sites in each segment were randomly selected (Figure 1). Fish were captured using a 4.3 m cataraft equipped with a Smith-Root (Vancouver, Washington, USA) 2.5 GPP Electrofisher with 0.8 m array droppers. The crew consisted of two netters at the bow of the raft and a rower. The electrofishing unit was set for direct current with a pulse rate of 120 pulses s^{-1} and 60% duty cycle. The number of sample sites surveyed varied annually (Figure 1) and by season and the amount of time electrofishing varied by visit (Table 1). Sample site length was 200 m in 2012, 100 m in the middle segment and 200 m in the upper segment in 2013, and 300 m in 2014. Site length was reduced in the middle segment in 2013 to ensure more sites were sampled in this less accessible segment. Site length was increased in 2014 to reduce the probability of temporary emigration during closed capture sampling (Gwinn et al. 2011). Sites usually were visited three times in each season in 2012 and 2013 and four times during a single season in 2014 (Table 1). At each visit, 1-2 sampling passes per site were conducted in the middle segment and 2-4 passes per site in the upper segment. Each pass moved downstream through a longitudinal section of the site. Constrained higher-gradient channels in the middle segment usually prevented returning upstream for additional passes. Additional passes were conducted in distinct longitudinal sections in the wider low-gradient channels of the upper segment. Electrofishing time was

recorded for each transect and totaled for each visit (Figure 3). Captured fish were held in a live well until the final pass of each site visit was completed. All fish were identified to species and measured for total length (mm). In 2014, large salmonids (i.e., >180 mm) were injected intraperitoneally with 12 mm halfduplex passive integrated transponder (PIT) tags during the first visit. In subsequent visits, large salmonids were scanned for PIT tags. If a tagged individual was recaptured, the tag code was recorded and the fish was released. If no tag was found, the fish was PIT-tagged prior to release. At the end of a site visit, all fish were released at the downstream end of the site. Fish surveys during the irrigation season were conducted from July to early October and encountered mean daily discharge ranging from 3.0 to $10.0 \text{ m}^3\text{s}^{-1}$ and water temperature ranging from 6.9 to 21.5°C in the middle segment and mean daily discharge ranging from 18.2 to $58.5 \text{ m}^3\text{s}^{-1}$ and water temperature ranging from 7.2 to 18.9°C in the upper segment (Figure 3). Fish surveys during the water storage season were conducted from mid-October to mid-December in 2012 and 2013 and March to mid-April in 2014 and encountered mean daily discharge ranging from 8.7 to $18.7 \text{ m}^3\text{s}^{-1}$ and water temperature ranging from 1.1 to 10.4°C in the middle segment and mean daily discharge ranging from 0.8 to $15.0 \text{ m}^3\text{s}^{-1}$ and water temperature ranging from 1.0 to 11.2°C in the upper segment (Figure 3).



Figure 3. Seasonal variability of discharge, water temperature, and electrofishing time during each site visit for all sites sampled during the study years (2012-2014). Number of visits for each site is shown below each electrofishing time boxplot. Boxplots describe median (center line), inner quartiles (boxes), 1.5*Interquartile range (whiskers), and outliers (points).

column represents the grouping of two or more factor levels into one.								
p-covariates	Description							
1	Constant p for all visits							
EfishTime	Electrofishing time per visit							
Season	Indicator variable for irrigation season							
SiteLn3	Site length classes (m): 100, 200, 300							
SiteLn2a	Site length classes (m): 100, 200=300							
SiteLn2b	Site length classes (m): 100=200,300							

Table 2. Description of covariates evaluated through occupancy and Nmixture modeling for their influence on detection (p), species occupancy (ψ), and mean site abundance (λ). The equals sign in the description

ψ-λ-covariates	Description
1	Constant ψ/λ across all sites
Reach	Different ψ/λ for each study reach
R1	Different ψ/λ by grouped reach: 1=2=3, 4=5
R2	Different ψ/λ by grouped reach: 1=2, 3=4=5
R3	Different ψ/λ by grouped reach: 1=2=4=5, 3
R4	Different ψ/λ by grouped reach: 1=2=3=5, 4
R5	Different ψ/λ by grouped reach: 1=2, 3, 4=5
SiteLn2a	Site length classes (m): 100, 200 (λ in 2013 only)
Year	Study year (ψ): 2012, 2013, 2014

Data analysis

Salmonid distribution and relative abundance was displayed graphically by plotting visit counts by site and size class. Small and large size classes were ≤ 180 and >180 mm, respectively (Figure 4). Using these size classes, small salmonids were generally younger than age-2 and large salmonids were age-2 and older (Pettit and Wallace 1975, Nuhfer 1988, Schroeder and Smith 1989).

There were three sampling designs used in this study: Dynamic occupancy, N-mixture, and closed capture. Dynamic occupancy modeling (MacKenzie et al. 2003) was used to estimate the probability of species occupancy (ψ), species detection (p), and site colonization and extinction among the study years for both size classes of each salmonid species. Hatchery-stocked fish were not included in any modeling. Model covariates were selected *a priori* for their potential influence on the estimators and included site-level covariates for site length, year, and reach (Table 2). The observation-level covariates were season and standardized electrofishing time (i.e., z-score). Site length and electrofishing time were analyzed separately because they were positively correlated (multiple R²=0.69). The year factor was used in modeling site colonization and extinction in the dynamic occupancy model. N-mixture modeling of count

data from repeated visits (Royle 2004) was used to jointly estimate mean site abundance (λ) and individual detection probability (p) for the large size class. In N-mixture modeling, each species in each year was modeled separately so the year factor was not included. Closed capture modeling (Otis et al. 1978) was used in 2014 to estimate abundance (\hat{N}) across sites sampled and site capture probability of individually marked salmonids. Closed capture modeling was conducted separately for each river segment and for the large size class of each salmonid species. Three basic closed-capture models were evaluated: 1) initial capture (p) and recapture (c) probabilities equal and constant across visits; 2) initial capture and recapture probabilities equal but vary by visit; and 3) initial capture and recapture probabilities differ, suggesting a behavioral response by individual animals after initial capture (i.e., attraction to or avoidance of boat electrofishing). Closed-capture abundance (\hat{N}), standard error (SE), and 95% confidence intervals were estimated through model-averaging.

Akaike information criterion model selection procedures were used with a correction factor for low sample size (AICc) to rank the models that best approximated the data. Models were ranked by AICc values and evaluated using the difference between a given model and the highest ranked model in AICc values (i.e., ΔAIC), and the relative measure of the weight of evidence for a model given the data (Burnham and Anderson 2002). The estimated parameters of each model were inspected for statistical significance ($\alpha < 0.05$); only models with informative (i.e., statistically significant) parameters were included in the ranking (Arnold 2010). Therefore, the best approximating model had the lowest AICc value, the greatest AICc weight, and informative parameters. In all modeling, species or individual detection probability models were fit first, holding the other estimator in the model constant; then the top detection model was used in the full analysis of the other estimator. Pearson χ^2 was used to assess the fit of N-mixture models and calculate the overdispersion parameter \hat{c} , which was reported for the final models and estimated using the R package AICcmodavg (Mazzerole 2017). Values of $\hat{c} > 1$ suggest either a moderate lack of model fit or unexplained variation in the count data (Kery and Royle 2016); $\hat{c} > 4$ suggests a poor fitting model (MacKenzie and Bailey 2004). Effective goodness-of-fit tests have not been developed for dynamic occupancy models (Kery and Royle 2016). Dynamic occupancy and N-mixture modeling and model selection procedures were completed using the R package unmarked (Fiske and Chandler 2011). Closed capture modeling, model averaging, and model selection procedures were conducted using Program MARK (White and Burnham 1999) via the package RMark (Laake 2008) in Program R (R Core Team 2017).

Precision, represented by the coefficient of variation (CV), was calculated using the equation: CV = SE/Estimate (Gerrodette 1993). Based on a power analysis using the program Trends (Gerrodette 1993), a

status estimator with $CV \le 0.25$ would be able to detect, with reasonable confidence (α =0.05, β =0.80), a 50% decline in the status estimator over a 25 year period sampling once every 5 years. This was used as a precision criterion with which to evaluate model estimates.



Figure 4. Length frequency of salmonids captured by reach during the entire study period. The middle segment was composed of reaches 1 and 2; the upper segment was composed of reaches 3, 4, and 5.

To obtain unbiased estimators, these sampling designs require that certain sampling assumptions are met (Otis et al. 1978). For occupancy modeling the assumptions are that sample sites are closed to changes in occupancy over the survey season, the probability of species detection and occupancy is constant across sites or differences are modeled by covariates, and species detection is independent at each survey location (McKenzie et al. 2006). The N-mixture model assumes net demographic closure of sites (i.e., site immigration and emigration are equal) during the sampling season, all variation in counts within a site is attributable to detection (Kery and Royle 2016), the distribution of animals across sample sites follows the Poisson distribution, and there is homogeneity of detection among all individuals present at a site during a survey so that the site detection probability represents a binomial trial of the true number of animals at that site (Royle 2004). The closure assumption for closed-capture sampling further requires the site be closed to any demographic change (i.e., no birth, death, immigration, or emigration of individuals) over the survey season. Channel width, discharge, and flow velocity were too great to allow for active site closure methods; therefore, it was assumed that sampling a site over a short time period during an annual study period (i.e., 1-4 months; Table 1) precluded site-level occupancy and net demographic changes (Pine et al. 2003). To meet the stricter site closure assumption of closed-capture abundance modeling in 2014, all four site visits were completed in 2-4 weeks (Table 1). Two additional assumptions (Otis et al. 1978) are required for closed-capture modeling: 1) fish do not lose their tags and 2) all tagged fish are correctly noted and recorded during each sampling visit. Captured fish were not double-marked so the former assumption was not tested. To reduce errors related to the latter assumption, field crews were careful recording PIT-tag information and interrogated every captured fish >180 mm in all visits subsequent to the first visit.

Results

Fish assemblage, distribution, and relative abundance

Redband Trout, Brown Trout, and Mountain Whitefish were captured in every site in at least one site visit over the three year study period (Figure 4). Redband Trout accounted for 11-26% of the annual catch in the middle segment and only 1-5% in the upper segment (Table 3). Relative abundance of Redband Trout was lowest in reach 4 (Figure 4, Figure 5). Most of the large Redband Trout captured in the upper segment were adipose fin-clipped hatchery fish (Table 3, Figure 4 and 5). Mountain Whitefish was the dominant species captured in all reaches of the Deschutes River study area (Figure 3), accounting for 60-72% of the annual catch in the middle segment and 63-94% in the upper segment (Table 3, Figure 4). Brown Trout composed 12-21% of the annual catch in the middle segment and 4-18% in the upper segment (Table 3). Brown Trout were most abundant in reaches 4 and 5. Brook Trout were captured only

in the middle segment and in low numbers (Table 3, Figure 4 and 5). Five other fish species were captured during boat electrofishing in the Deschutes River (Table 3).

Species detection and occupancy modeling

The best approximating detection and occupancy models varied among the salmonid species (Table 4). Season and site length generally were important factors explaining variation in species detection in an occupied site (Table 4). Detection probability was higher during the irrigation season for small and large



Figure 5. Relative abundance and distribution of salmonids by size class and for all visits in 2012-2014. Boxplots summarize salmonid counts by visit for each site and describe the median (center line), inner quartiles (boxes), 1.5*Interquartile range (whiskers), and outliers (points).

Redband Trout and small Mountain Whitefish (Table 5). Specifically, the probability of detection of large Redband Trout was more than two times greater during the irrigation season (p=0.82) than during the storage season (p=0.39) (Table 5). Detection probability generally increased with site length or electrofishing time for both size classes of each species, except for large Redband Trout (Table 5). The smaller size classes generally had lower detection probabilities than the larger size classes (Table 5). Reach spatial groupings were important factors explaining variation in occupancy of large Redband Trout and small Brown Trout (Table 4). The probability of large Redband Trout occupying a site was lowest in reach 4 (ψ =0.41) relative to the other reaches (ψ =0.90) (Table 5). The occupancy probability of small Brown Trout was especially low ($\psi = 0.12$) in the middle segment (Table 5). The occupancy probability of small Redband Trout throughout the study area and period was 0.77, as year and spatial factors were not important explanatory covariates for these data (Table 5). Occupancy probability estimates were relatively precise for small Redband Trout among reaches (CV=0.13) and large Redband Trout in reaches 1, 2, 3, and 5 (CV=0.11) but relatively imprecise for large Redband Trout in reach 4 (CV=0.47). Occupancy estimates were relatively precise for small Mountain Whitefish, small Brown Trout in the upper segment, and large Brown Trout (CV range, 0.04-0.09), but the estimate was relatively imprecise for small Brown Trout in the middle segment (CV=0.94).

		201	2	201	3	201	4	To	tal Leng	gth (mr	n)
Study Segment	Species	Ν	%	Ν	%	Ν	%	Mean	SD	Min	Max
Middle	Mountain Whitefish	494	67	590	72	1004	60	221	97	65	442
Deschutes	Redband Trout (Wild)	83	11	89	11	436	26	187	44	50	403
River	Brown Trout	158	21	132	16	193	12	247	83	70	555
	Sculpin species ¹	0	0	7	1	14	1	82	13	34	98
	Tui Chub ²	1	0	2	0	12	1	123	39	66	195
	Brown Bullhead ³	1	0	4	0	1	0	175	31	135	209
	Brook Trout ⁴	0	0	0	0	4	0	257	80	160	345
Three-spined Stickleback		2	0	0	0	2	0	34	4	30	39
	Kokanee ⁶	0	0	0	0	2	0	110	0	110	110
Upper	Mountain Whitefish	2313	63	3072	69	3520	94	222	79	79	483
Deschutes	Redband Trout (Wild)	124	3	236	5	53	1	147	81	56	602
River	Redband Trout (Hatchery)	26	1	45	1	6	0	273	48	170	420
	Brown Trout	634	17	777	18	160	4	209	132	50	635
	Sculpin species	228	6	183	4	0	0	58	18	26	107
	Tui Chub	22	1	26	1	0	0	92	47	40	191
	Brown Bullhead	28	1	30	1	4	0	187	59	52	325
	Three-spined Stickleback	251	7	42	1	0	0	45	26	19	440
	Kokanee	28	1	16	0	0	0	123	64	44	360

Table 3. Boat electrofishing counts (*N*) of all fish captured and as a percentage of the total catch within the study segment (%) in the middle and upper Deschutes River in all study years (2012-2014). Hatchery stocked Redband Trout were determined by the absence of an adipose fin.

¹Cottus ssp, ²Gila bicolor, ³Catostomus columbianus, ⁴O. nerka, ⁵Gasterosteus aculeatus, ⁶Ameiurus nebulosus

Table 4. Dynamic occupancy model selection results for two size classes of three salmonid species in the Deschutes River study area from 2012 through 2014. Model selection for detection probability (p) and occupancy probability (ψ) was conducted using Akaike Information Criterion with a correction for small sample size (AICc). Models were ranked by AICc score and relative weight of evidence (Wt) and described by covariates (see Table 2), number of parameters, and difference in score (Δ AICc) between the top (in bold) and lower-ranked models. Only models with informative parameters are shown ($\alpha < 0.05$). Occupancy was at or near 1.00 for large mountain whitefish and, as a result, the full model did not converge (NC).

Species	p-Models	Param.	AICc	ΔAICc	Wt	ψ-Models	Param.	AICc	ΔAICc	Wt
Small	~Season+SiteLn2a	6	508.9	0.0	1.00	~1	6	508.9	0.0	1.00
Small Redband	~Season	5	521.8	12.9	0.00					
Trout	~SiteLn2a	5	530.7	21.8	0.00					
mout	~EfishTime	5	535.7	26.8	0.00					
	~SiteLn3	6	445.7	0.0	1.00	~R2	7	430.7	0.0	1.00
C 11	~Season+SiteLn2b	6	478.1	32.3	0.00	~1	6	445.7	15.1	0.00
Small Brown	~Season+SiteLn2a	6	488.4	42.7	0.00					
Trout	~SiteLn2a	5	493.6	47.9	0.00					
	~Season	5	505.7	60.0	0.00					
	~1	4	511.0	65.3	0.00					
	~Season+SiteLn2a	6	617.6	0.0	0.77	~Year	8	610.5	0.0	0.97
Small	~Season	5	620.0	2.5	0.23	~1	6	617.6	7.1	0.03
Mountain	~1	4	631.3	13.7	0.00					
Whitefish	~SiteLn2b	5	632.7	15.1	0.00					
	~SiteLn2a	5	670.0	52.4	0.00					
Large	~Season	5	535.2	0.0	1.00	~R4	6	532.4	0.0	1.00
Redband	~SiteLn2b	5	574.8	39.6	0.00					
Trout	~SiteLn2a	5	576.6	41.4	0.00					
	~SiteLn3	6	579.8	0.0	0.50	~1	6	579.8	0.0	1.00
Large	~EfishTime	5	580.1	0.3	0.43					
Brown	~SiteLn2b	5	584.1	4.3	0.06					
Hout	~1	4	587.8	8.0	0.01					
	~SiteLn2a	5	595.1	15.3	0.00					
		F	221.0	0.0	0.00	NG				
	~EfishTime	2	331.9	0.0	0.98	NC				
Large	~SiteLn3	6	340.1	8.5	0.02					
Mountain Whitefich	~SiteLn2b	5	348.5	16.6	0.00					
winterish	~SiteLn2a	5	350.2	18.3	0.00					
	~1	4	405.7	73.8	0.00					

N-mixture individual detection and site abundance modeling

The best approximating N-mixture models for individual detection and mean site abundance for large fish varied among the salmonid species. Electrofishing time or site length was positively related to detection probability and helped explain variation in detection probability for most years and all three species (Tables 6 and 7). Detection probability at the mean electrofishing time among years was relatively low for Redband Trout (range in means in p, 0.09-0.11), moderate for Brown Trout (range, 0.01-0.20), and highest for Mountain Whitefish (p=0.33) (Table 7). Season was an important factor explaining variation in detection in Redband Trout in 2013 and Mountain Whitefish in 2012 and 2013 (Table 6). Reach was an

important spatial factor explaining variation in mean site abundance (λ) for all species (Table 6) and the spatial patterns of abundance generally were consistent among the study years (Table 7). Mean site abundance of Redband Trout was generally higher in reaches 1, 2, and 3 (annual λ , 8-12) and lower in reaches 4 and 5 (annual λ , 1-3). For Brown Trout, mean site abundance was higher in reach 1, 2, 4, 5 (annual λ , 9-16) and lower in reach 3 (annual λ , 4-9). Mean site abundance of Mountain Whitefish was generally higher in reaches 3, 4, and 5 (annual λ , 48-142) and lower in reaches 1 and 2 (annual λ , 18-56). Mean site abundance estimates were relatively imprecise for Redband Trout (CV range, 0.42-0.93) and Brown Trout (CV range, 0.14-1.17) and relatively precise for Mountain Whitefish (CV range, 0.04-0.15) (Table 7). The N-mixture models used to produce Redband Trout and Brown Trout estimators showed either a low-to-moderate lack of fit or unexplained variation in the count data that was not accounted for by the model (\hat{c} range, 1.2-2.1); except for the estimates for Brown Trout in 2012 (\hat{c} , 4.1), which showed that this model did not fit the data well (Table 7). The Mountain Whitefish models showed a severe lack of fit to the data (\hat{c} range, 4.0-13.0) (Table 7).

Table 5. Detection (p) and occupancy (ψ) probability estimates with 95% confidence intervals (CI) and linear
modeling results for two size classes of three salmonid species in the upper Deschutes River study area from
2012 through 2014.

				95%	6 CI				95%	6 CI	
Species	Covariate Levels	p- Estimate	SE	Lower	Upper	Covariate Levels	ψ- Estimate	SE	Lower	Upper	CV
Small	Storage + 100m	0.06	0.03	0.02	0.15	Reach 1,2,3,4,5	0.77	0.10	0.52	0.91	0.13
Redband Trout	Storage + 200-300m	0.45	0.04	0.37	0.53						
	Irrigation + 100m	0.20	0.09	0.08	0.43						
	Irrigation + 200-300m	0.76	0.04	0.66	0.84						
Small	100m	0.10	0.04	0.04	0.22	Reach 1,2	0.12	0.12	0.02	0.54	0.94
Brown Trout	200m	0.80	0.03	0.73	0.86	Reach 3,4,5	0.92	0.06	0.68	0.98	0.07
	300m	0.34	0.05	0.25	0.45						
Small	Storage + 100m	0.56	0.07	0.43	0.68	2012	0.93	0.05	0.83	0.99	0.06
Mountain	Storage + 200-300m	0.69	0.03	0.64	0.74	2013	0.76	0.07	0.62	0.89	0.09
Whitefish	Irrigation + 100m	0.77	0.07	0.61	0.88	2014	0.95	0.03	0.88	0.99	0.04
	Irrigation + 200-300m	0.86	0.04	0.77	0.92						
Large	Storage	0.39	0.04	0.31	0.46	Reach 1,2,3,5	0.90	0.10	0.50	0.99	0.11
Redband Trout	Irrigation	0.82	0.04	0.72	0.89	Reach 4	0.41	0.19	0.13	0.76	0.47
Large	100m	0.59	0.07	0.46	0.71	Reach 1,2,3,4,5	0.92	0.06	0.70	0.98	0.06
Brown Trout	200m	0.76	0.03	0.69	0.82						
	300m	0.81	0.03	0.75	0.85						
Large	100m	0.72	0.05	0.62	0.80	Reach 1,2,3,4,5	NC				
Mountain	200m	0.88	0.02	0.83	0.92						
Whitefish	300m	0.97	0.01	0.94	0.99						

Table 6. N-mixture model selection results for three salmonid species in the Deschutes River study area from 2012 through 2014. Model selection for detection probability (p) and mean site abundance (λ) was conducted using Akaike Information Criterion with a correction for small sample size (AICc). Models were ranked by AICc score and relative weight of evidence (Wt) and described by covariates (see Table Covs), number of parameters, and difference in score between top (in bold) and lower ranked models. The models shown are only those whose linear coefficients were statistically significant ($\alpha < 0.05$).

		D	etection mode	1 selection		Mean site abundance model selection						
Species	Year	p-Models	Param.	AICc	ΔAICc	Wt	λ-Models	Param.	AICc	ΔAICc	Wt	
	2012	~EfishTime	3	275.5	0.0	0.81	~R2	4	266.2	0.0	0.69	
		~Season	3	278.8	3.3	0.15	~R5	5	268.2	2.0	0.25	
		~1	2	281.6	6.0	0.04	~R1	4	271.3	5.1	0.05	
							~1	3	275.5	9.3	0.01	
Ŧ	2013	~Season	3	450.8	0.0	0.91	~R4	4	434.4	0.0	1.00	
Trou		~1	2	455.4	4.6	0.09	~R3	4	449.4	15.0	0.00	
and							~1	3	450.8	16.4	0.00	
Redb	2014	~1	2	140.4	0.0	0.57	~R5	3	120.8	0.0	0.73	
		~EfishTime	3	141.0	0.6	0.43	~Reach	4	122.7	2.0	0.27	
							~R4	3	135.6	14.8	0.00	
							~1	2	140.4	19.6	0.00	
	2014	~EfishTime	3	351.3	0.0	1.00	~1	3	351.3	0.0	0.71	
		~1	2	402.4	51.0	0.00	~Reach	4	353.2	1.8	0.29	
	2012	~EfishTime	3	650.0	0.0	1.00	~R3	4	625.7	0.0	1.00	
Trout		~1	2	758.3	108.3	0.00	~R1	4	643.0	17.3	0.00	
							~1	3	650.0	24.3	0.00	
	2013	~SiteLn2a	3	796.1	0.0	0.77	~R3	4	778.7	0.0	0.79	
		~EfishTime	3	798.5	2.5	0.23	~R1	4	781.4	2.7	0.21	
'nwu		~1	2	829.5	33.5	0.00	~1	3	796.1	17.4	0.00	
Brc	2014	~1	2	271.1	0.0	0.63	~R5	3	267.5	0.0	0.63	
		~EfishTime	3	272.2	1.0	0.37	~Reach	4	269.2	1.7	0.27	
							~1	2	271.1	3.6	0.10	
	2014	~EfishTime	3	281.6	0.0	0.75	~1	3	281.6	0.0	0.70	
		~1	2	283.9	2.2	0.25	~Reach	4	283.3	1.7	0.30	
	2012	~Season	3	1627.4	0.0	1.00	~Reach	7	1460.3	0.0	1.00	
		~EfishTime	3	1658.7	31.3	0.00	~R5	5	1494.8	34.5	0.00	
		~1	2	1665.8	38.4	0.00	~R2	4	1495.1	34.8	0.00	
							~R1	4	1548.8	88.5	0.00	
							~R4	4	1555.3	95.0	0.00	
							~R3	4	1625.8	165.5	0.00	
fish	2012	G	4	20(1.5	0.0	1.00	~1	5	1027.4	167.1	1.00	
hite	2015	~Season+SiteLn2a	4	2061.5	0.0	1.00	~R2	5	2032.7	0.0	1.00	
N II		~Ensnume+Season	4	2100.5	105.0	0.00	~K4	5	2056.5	23.9	0.00	
untai		~SheLliza	2	2255.9	220.1	0.00	~1	4	2001.5	28.9	0.00	
Moi		~Season	2	2300.0	259.1	0.00						
		Ensiri mie	3 2	2510.0	441.2	0.00						
	2014	- I	2	1350.3	0.0	1.00	P4	Λ	1326.5	0.0	1.00	
	2014	-Lusu i nne	3 2	1302.1	42.0	0.00	~ R 4	4 1	1320.5	21.1	0.00	
			2	1595.1	42.9	0.00	~1	4	1347.0	21.1	0.00	
	2014	~FfichTime	3	550.9	0.0	0.81	~Reach	3	542.4	23.0	0.00	
	2014	~1	2	553.8	2.0	0.19	~1	7	550.0	8.5	0.99	
	1	1	4	555.0	2.7	0.17	1	5	550.7	0.5	0.01	

					95% CI					95% CI			
	Year	Covariate Levels	p-Estimated	SE	Lower	Upper	Covariate Levels	λ-Estimated	SE	Lower	Upper	CV	c-hat
	2012	EfishTime: min	0.06	0.03	0.02	0.15	Reach 1,2	9	5	3	26	0.55	1.9
		EfishTime: mean	0.11	0.06	0.03	0.30	Reach 3,4,5	3	2	1	11	0.63	
		EfishTime: max	0.46	0.29	0.08	0.89							
ıt	2013	Storage	0.06	0.03	0.02	0.15	Reach 1,2,3,5	8	4	3	20	0.49	1.4
lrou		Irrigation	0.09	0.05	0.03	0.24	Reach 4	2	1	1	5	0.58	
L pu	2014	Constant	0.10	0.08	0.02	0.42	Reach 3	12	10	2	65	0.87	1.8
Redba	(Storage season, upper segment)						Reach 45	1	1	0	9	0.93	
	2014	EfishTime: min	0.04	0.02	0.02	0.10	Reach 1,2	28	12	12	64	0.42	2.1
	(Irrigation	EfishTime: mean	0.09	0.04	0.04	0.19							
	season, middle segment)	EfishTime: max	0.52	0.16	0.23	0.80							
	2012	EfishTime: min	0.08	0.01	0.05	0.11	Reach 3	4	1	2	8	0.33	4.1
		EfishTime: mean	0.22	0.03	0.17	0.29	Reach 1,2,4,5	15	2	11	20	0.14	
		EfishTime: max	0.90	0.05	0.74	0.96							
	2013	100m	0.06	0.02	0.03	0.11	Reach 3	5	2	2	11	0.39	1.6
rout		200-300m	0.14	0.05	0.07	0.27	Reach 1,2,4,5	16	5	9	28	0.30	
n Tı	2014	Constant	0.14	0.10	0.03	0.46	Reach 3,4,5	9	7	2	40	0.79	1.3
Brow	(Storage season, upper segment)												
	2014	EfishTime: min	0.11	0.06	0.03	0.31	Reach 1,2	13	7	4	40	0.54	1.2
	(Irrigation	EfishTime: mean	0.14	0.08	0.04	0.40							
	season, middle segment)	EfishTime: max	0.31	0.21	0.06	0.75							
	2012	Storage	0.20	0.01	0.17	0.23	Reach 1	27	4	21	36	0.14	10.6
		Irrigation	0.16	0.01	0.13	0.18	Reach 2	56	6	45	70	0.11	
							Reach 3	90	9	74	109	0.10	
							Reach 4	113	8	97	131	0.07	
_							Reach 5	84	8	70	102	0.10	
fish	2013	Storage+100m	0.13	0.02	0.10	0.18	Reach 1,2	18	3	13	24	0.15	7.5
hite		Storage+200-300m	0.18	0.01	0.15	0.21	Reach 3,4,5	48	4	41	56	0.08	
Ν		Irrigation+100m	0.24	0.03	0.18	0.32							
ntain		Irrigation+200-300m	0.31	0.02	0.27	0.36							
Iour	2014	EfishTime: min	0.22	0.02	0.19	0.25	Reach 4	142	6	130	154	0.04	13.0
N	(Storage season,	EfishTime: mean	0.33	0.01	0.30	0.35	Reach 3,5	110	6	100	122	0.05	
	upper segment)	EfishTime: max	0.43	0.02	0.39	0.48							
	2014	EfishTime: min	0.27	0.04	0.19	0.36	Reach 1	19	3	14	25	0.15	4.0
	(Irrigation	EfishTime: mean	0.33	0.04	0.25	0.42	Reach 2	28	4	21	37	0.15	
	season, middle segment)	EfishTime: max	0.58	0.12	0.35	0.78							

Table 7. Mean site abundance (λ) and detection probability (p) estimated using the N-mixture model for large salmonids in the Deschutes River study area.

Closed-capture modeling of individual capture probability and abundance

Overall, 1048 large salmonids were PIT-tagged over the 4 visits to the Deschutes River sample sites in 2014 and only 33 fish were recaptured on a subsequent visit (Table 8). Mean lengths of tagged fish ranged from 219-394 mm TL (Table 8). In the middle Deschutes River (i.e., reaches 1 and 2), the best approximating closed-capture model for Redband Trout and Brown showed a behavioral response to tagging (Tables 9 and 10), with higher initial capture probabilities (p=0.166 and p=0.178, respectively) than recapture probabilities (c=0.014 and c=0.030, respectively) that did not vary by visit (Table 9 and 10). Individual capture and recapture probabilities of Mountain Whitefish in the middle segment were equally low and constant across visits (p=0.027). In the upper segment, only 26 large Redband Trout were captured and none were recaptured, which precluded abundance estimation. The best approximating closed-capture model for Brown Trout and Mountain Whitefish in the upper segment showed initial and recapture probabilities to be equal and varying over the visits (Table 8). For these two species, the individual capture probability was low in the first two visits (p range, 0.016-0.033) and decreased in the third and fourth visits (p range, 0.011-0.020) (Table 10). The abundance estimates in the 20 sites in the middle segment were 1153 (i.e., 57 per site) for Redband Trout, 461 (23 per site) for Brown Trout, and 1774 (89 per site) for Mountain Whitefish. The abundance estimates in the 21 sites in the upper segment were 1212 (58 per site) for Brown Trout, and 4252 (202 per site) for Mountain Whitefish (Table 10). These abundance estimates were relatively imprecise (CV range, 0.46-1.51). There was direct evidence that the site-closure assumption was violated: one Mountain Whitefish was tagged in site Tumalo 7 and recaptured on the same day in the downstream adjacent site Tumalo 8 and another was tagged in site Tumalo 7 and captured two weeks later upstream in site Tumalo 5.

Segment	Species	Tagged (N)	Recaptured (N)	Mean TL	SD	Min	Max
Middle	Redband Trout	214	5	219	31	181	377
	Brown Trout	136	7	274	89	181	495
	Brook Trout	3	0	289	58	229	345
	Mountain Whitefish	222	9	302	58	183	442
Upper	Redband Trout	26	0	254	57	185	446
	Brown Trout	127	4	394	78	186	560
	Mountain Whitefish	320	8	277	37	185	416

Table 8. PIT tagging results for salmonids (\geq 140 mm) in the Deschutes River study area in 2014. Mean total length (TL) and its standard deviation (SD), minimum, and maximum are in mm.

Segment	Species	Model	Param.	AICc	ΔAICc	Weight	Deviance	Description
Middle	Redband Trout	p(~1)c(~1)	3	-1225.0	0.0	0.77	23.0	Behavioral response to initial capture, not time varying
		p(~visit)c()	5	-1222.1	2.9	0.18	21.8	
		p(~1)c()	2	-1219.7	5.3	0.05	30.3	
	Brown Trout	p(~1)c(~1)	3	-624.6	0.0	0.74	13.4	Behavioral response to initial capture, not time varying
		p(~1)c()	2	-622.1	2.5	0.22	17.9	
		p(~time)c()	5	-619.0	5.6	0.05	14.9	
	Mountain Whitefish	p(~1)c()	2	-1252.4	0.0	0.63	17.7	Initial capture and recapture probabilities equal, constant across visits
		p(~1)c(~1)	3	-1251.0	1.4	0.31	17.1	
		p(~visit)c()	5	-1247.6	4.8	0.06	16.5	
Upper	Redband Trout	NA	NA	NA	NA	NA	NA	No tagged fish were recaptured
	Brown Trout	p(~visit)c()	5	-594.6	0.0	0.78	10.7	Capture probability varied with visit
		p(~1)c(~1)	3	-592.1	2.5	0.22	17.2	
		p(~1)c()	2	-581.5	13.1	0.00	29.9	
	Mountain Whitefish	p(~visit)c()	5	-2074.0	0.0	0.76	23.0	Capture probability varied with visit
		p(~1)c()	2	-2071.0	3.0	0.17	32.1	
		$p(\sim 1)c(\sim 1)$	3	-2069.2	4.8	0.07	31.9	

Table 9. Closed-capture models evaluated using Akaike's Information Criterion with a correction for small	
sample size (AICc) for three salmonid species in two segments of the Deschutes River in 2014. The best	
approximating model, determined by its Akaike weight, is described. No tagged redband trout were recaptured i	n
the upper segment, which precluded modeling.	

Discussion

The two objectives of this study were to evaluate sampling designs for the reliability of their estimators and feasibility of their sampling method to monitor trends in the Redband Trout and other salmonid populations and to determine the current status of Redband Trout and other salmonids in the middle and upper Deschutes River. Criteria for a reliable and feasible sampling design are that it provides precise and unbiased estimates of population status, the sample is composed of an adequate number of representative sites, and the sampling method is low enough cost and has the fewest possible logistical constraints that it can be implemented repeatedly over time. Using these criteria, this study showed that estimates of Nmixture mean site abundance (λ) and closed capture abundance (\hat{N}) were too imprecise and likely biased to be effective as status estimators for monitoring trend in this study area. In contrast, estimates of occupancy probability (ψ) in this study area were relatively precise and probably unbiased since the occupancy sampling assumptions are relatively easier to meet. There were some weaknesses and logistical constraints of boat electrofishing in large river habitat that affected these estimators and how representative the sampling frame was of the study area; however, with some improvements in the sampling method, occupancy estimation met the above criteria and may be useful to managers as a long-term monitoring sampling design for tracking trends in occupancy and relative abundance of Redband Trout and other salmonids in the middle and upper Deschutes River.

Table 10. Capture (p) and recapture (c) probability and model averaged abundance (\hat{N}) estimated for fish >180 mm total length from the top closed-capture models for each salmonid species in 2014. None of the 26 redband trout tagged in the upper segment were recaptured, which precluded abundance estimation.

Segment	Species	Parameter	Estimate	SE	L: 95%	U: 95%	CV
Middle	Redband	p-Constant	0.166	0.052	0.087	0.293	
Deschutes	Trout	c-Constant	0.014	0.006	0.006	0.032	
River		\widehat{N}	1133	1715	251	22772	1.51
	Brown Trout	p-Constant	0.178	0.064	0.084	0.338	
		c-Constant	0.030	0.011	0.014	0.061	
		\widehat{N}	461	545	163	3968	1.18
	Mountain	p=c, Constant	0.027	0.009	0.014	0.050	
	Whitefish	\widehat{N}	1774	1122	720	5060	0.63
Upper	Redband	c, Constant	0.000	NA	NA	NA	
Deschutes	Trout	\widehat{N}	NA	NA	NA	NA	NA
River							
	Brown Trout	p1	0.026	0.013	0.010	0.069	
		p2=c2	0.033	0.016	0.012	0.085	
		p3=c3	0.017	0.009	0.006	0.047	
		p4=c4	0.011	0.006	0.004	0.032	
		\widehat{N}	1212	977	369	5112	0.81
	Mountain	p1	0.016	0.006	0.008	0.032	
	Whitefish	p2=c2	0.023	0.008	0.012	0.045	
		p3=c3	0.020	0.007	0.010	0.038	
		p4=c4	0.016	0.005	0.008	0.031	
		\widehat{N}	4252	1940	2073	9138	0.46

Precision

The reliability of a sampling design to track a trend in status depends on how precisely a status estimator can be measured and how close on average (i.e., unbiased) the status estimator is to the true parameter under study (Conroy and Carroll 2009). The precision of status estimates in this study was compared to a reach-level precision criterion relevant to reliable monitoring (i.e., $CV \le 0.25$), which has been used elsewhere to evaluate large river sampling designs for monitoring fish populations (e.g., Gwinn et al. 2011). Closed-capture abundance estimates in this study were highly imprecise (CV range, 0.46-1.51) and did not meet the precision criterion for effectively detecting trend in status. Precision was especially low for the target species Redband Trout (CV=1.51). Mean site abundance (λ) estimates of Redband Trout again showed the worst precision of the three species and did not meet the precision criterion (CV range, 0.42-0.93). The precision of abundance estimates for Brown Trout did not meet the criterion (CV range, 0.30-0.79), except for the estimate in 2012 (CV=0.14). Mountain whitefish abundance estimates were relatively precise (CV < 0.15), but these N-mixture models and the one that provided a relatively precise Brown Trout estimate showed a general lack of fit (\hat{c} range, 4.0-13.1) and likely underestimated the actual variation in the data (Kery and Royle 2016). In contrast, the precision of the occupancy (ψ) estimates were much better for all species and size classes (CV range, 0.04-0.13) and, with two exceptions, met the precision criterion for effectively detecting a trend in status. In the exceptional cases, the relative imprecision of the occupancy estimate was likely due to low sample size for a single reach estimate (N=10) for large Redband Trout in reach 4 (CV=0.47) and low detection probability in certain years (p=0.10 in 2012 and p=0.34 in 2014) for small Brown Trout in the middle segment (CV=0.94).

The two main factors influencing estimator precision are sample size and species or individual detection probability (Conroy and Carroll 2009). Higher sample size and detection probability lead to lower standard error of an estimator. As shown above, species detection in occupancy sampling provided more precise status estimates compared to individual detection required of abundance sampling. Within a given sample site, it is generally easier to detect the presence of a species than it is to recapture an individually marked fish. In this study, species detection was relatively high in occupancy sampling for the large size class during the irrigation season (p range, 0.59-0.97). For N-mixture sampling, individual detection probabilities usually depended on the related covariates electrofishing time or site length but overall were relatively low for the large size class of all three species (p range, 0.09-0.33). In closed capture sampling, recapture probabilities were extremely low for all species (c range, 0.000-0.033); and those of Redband Trout were the lowest (c range, 0.000-0.017).

Given the many challenges of sampling in large river habitats, it is not surprising that capture probabilities using the closed capture sampling design were low, but it is not clear why they were so low in this study. A pilot study using similar sampling methods (e.g., repeated site visits, uniquely tagging fish, and boat electrofishing) in Deschutes River sites just downstream of this study area were marginally better (p=0.03-0.07), but still so low they resulted in imprecise abundances estimates (Jacobsen and Jacobs 2010). Other monitoring studies using closed-capture sampling methods to estimate Rainbow Trout abundance in larger rivers have ranged in individual detection probability from 0.09 using angling as a capture method in the Kisaralik River (36 m channel width; Harper et al. 1997) to 0.12 and 0.15 using boat electrofishing in the Spokane River (13.3 m³s⁻¹; Lee 2013). In a multi-year closed-capture study to estimate Smallmouth Bass Micropterus dolomieu abundance in a large river (50 to 165 m channel width) in Virginia, using boat electrofishing in the main channel and backpack electrofishing in the shallow areas, annual capture probability ranged from 0.11 to 0.57 (median, 0.36; Odenkirk and Smith 2005). When closed-capture methods were used in a Brown Trout removal study in the smaller Logan River (14 m wetted width, 3 m³s⁻¹ baseflows), capture probabilities using a canoe-mounted electrofisher were greater (range, 0.29-0.95; Saunders et al. 2014). The results of this study and previous studies suggest that the capture probability of individual salmonids is too low using a single boat electrofisher as the sole sampling method in a river the size of the Deschutes River to result in reliable abundance estimates.

Bias

It is also possible that capture probabilities did not reflect the true likelihood of capturing an individual fish and biased the abundance estimates. The primary evidence for bias was that estimates of \hat{N} , after converting them into mean site abundance, were substantially larger than the estimates of λ for all species and in both segments in 2014, which was the only study year in which both sampling designs were implemented. Given the low precision of these estimates, the difference in these estimates may not be statistically significant, but the consistent tendency of the difference suggests one or both may be biased. The main source of potential bias in \hat{N} was violation of the closure assumption; in particular, net emigration from the site, which would bias detection low and overestimate abundance. Two Mountain Whitefish were tagged in one site and recaptured in nearby sites, one upstream and one downstream, during subsequent visits, providing direct evidence of violating the site closure assumption. Moreover, individual detection probability estimates may have been biased low for two reasons. First, at the end of a sampling visit, the field crew released all tagged fish at the downstream end of the sample site, which may have led to net emigration from a site during a season. Captured fish were not released near the capture locations within the site because of the logistical difficulties in getting back upstream in the boat or on

foot on the river in the steep and constrained middle segment. Second, the highest ranked closed capture models for Redband Trout and Brown Trout showed relatively high initial capture probabilities and extremely low recapture probabilities. This usually implies behavioral avoidance of recapture, but in this case the recapture probabilities may have been biased low because of net emigration due to the sampling methods. Other assumptions that were potentially violated included tag loss (which was not estimated through double-tagging in this study) and missed tags through inadequate scanning of captured fish with the PIT tag reader; if either were violated, these would further bias capture probability low. Together, this potential bias toward lower capture probabilities suggests that closed capture abundance was likely overestimated in this study.

Net emigration from a site during a season also would violate the closure assumption for N-mixture modeling and lead to individual detection probabilities biased low and λ estimates biased high. However, a caveat with the N-mixture sampling design is that there may be a proportion of the fish population in a site that is at least temporarily unavailable to detection (Couturier et al. 2013). Generally, the farther an individual fish is from the electric field of the electrofisher, the less detectable that fish becomes (Efford and Dawson 2009). This may be exacerbated in large river habitats like the Deschutes River, in which a proportion of the population may be temporarily outside the reach of the boat electrofisher, either at depths or in longitudinal sections that were outside of the reach of the electric field. The unknown proportion of the population unavailable to detection would not be included in the estimate of λ and the estimate would be biased low relative to the true population. A tendency of the N-mixture sampling design to underestimate true abundance has been noted in other studies (Couturier et al. 2013) and suggests that true abundance may lie somewhere between λ and \hat{N} .

Sampling method

Potential bias, low individual detection probability, and low precision of λ and \hat{N} estimates strongly suggest that, if these estimators are used in future monitoring of Redband Trout in rivers of similar size to this Deschutes River segment, substantial changes to the sampling methods used in this study will be needed to ensure that these sampling designs reliably estimate status. The changes would affect survey timing (i.e., season), site length, sample size and distribution, and capture methods.

Survey time period was an important factor influencing species and individual detection and the number of Redband Trout and Brown Trout captured. Throughout the study area, the detection probability of Redband Trout of both size classes was 1.5 to 3 times higher during the irrigation season from July through September than during the storage season from November through April. In 2014, the total

number of Redband Trout and Brown Trout captured in the upper segment in March and April declined by 76% and 79%, respectively, relative to total counts from sampling in July through September in 2013. In contrast, total counts from July through September sampling in the middle segment in 2014 increased substantially for all three salmonid species, which was expected given the increase in site length in both segments to 300 m in 2014. Lower detection probability and fish counts in a particular season suggest that environmental conditions and life cycle timing may have influenced seasonal patterns of occupancy and abundance or seasonal fish behavior and concomitant effects on fish detection probability, or both. Therefore, sampling season needs to be considered in light of these factors to determine the best time to conduct surveys. Given that higher detection leads to greater estimator precision, July-September was the best time to conduct this sampling method for Redband Trout in this study area.

Site length was an important factor in detection probability estimated by occupancy and N-mixture sampling designs; with longer site length, or greater electrofishing time, leading to a higher probability of detection of species or individuals present at a site. (Site length was not evaluated in the closed capture sampling design because it was only used in 2014, in which all sites were 300 m long.) In the occupancy sampling design, increasing from 100 m to 200 m site length influenced detection more than the increase from 200 m to 300 m sites for most species and size classes. In the N-mixture and closed-capture sampling designs, 300 m site length was not enough to obtain precise abundance estimates. As discussed above, this failure may be affected by the sampling method protocol causing net emigration from sites and biasing detection, and it may be affected by temporary emigration by fish with seasonal home ranges larger than the site (Gwinn et al. 2011). In a simulation using Murray Cod Maccullochella peelii and their known home ranges in a large Australian river, Gwinn et al. (2011) estimated that to achieve an acceptable abundance estimate using four site visits during a survey season, sample sites would have to be at least 1400 m long. Home range length, temporary emigration rates, and the ideal site length are currently not known for Redband Trout in the Deschutes River. These results suggest that 200-300 m sites are long enough to produce reliable occupancy estimates, but site length may need to be substantially longer for the sampling designs that estimate abundance.

Within the 150 km Deschutes River study area, there were only 42 sample sites and 5-11 sites in individual reaches. This relatively small sample size likely contributed to the low precision of the status estimates and prevented the evaluation of models with more covariates. Furthermore, logistical and safety constraints prevented the use of boat electrofishing in 10-15 km long sections within each study reach, which precluded a spatially balanced sample. This relatively small sample size and unbalanced site distribution calls into question the representativeness of the sample to the true population. Additionally, in

the middle segment, most of the sites that were accessible to the boat were sampled with a single longitudinal pass down the main flow line or the deepest part of the channel because channel slope and water velocity prevented the boat from returning upstream for another pass. As a result, sampling was minimal in the juvenile rearing habitats (e.g., river margins, secondary channels) in the middle segment, few fish less than 120 mm TL were captured, and the occupancy probability of the small size class may be underestimated for trout. In order to make inferences to the entire study area and all parts of the channel, future monitoring plans need to incorporate a larger, more representative sample and explore the use of additional and alternative sampling gear types (Grabow et al. 2009) to ensure that all sections of the study area and channel are accessible to the survey.

Status

Although Redband Trout and the other species were distributed throughout the Deschutes River study area, there were distinct spatial patterns in occupancy and relative abundance. One spatial pattern showed that Redband Trout have a lower status in the upper two sampling reaches (i.e., upstream from the Spring River confluence to Wickiup Dam) relative to other salmonids in these reaches and Redband Trout in the lower three reaches. This pattern was especially stark in reach 4 (Spring River to Wickiup Dam) in which large Redband Trout had relatively low probability of occupancy (ψ =0.41) and low relative abundance. In contrast, large Brown Trout had a much higher occupancy probability (ψ =0.92) and relative abundance in reaches 4 and 5. In the middle segment, Redband Trout were in higher relative abundance than Brown Trout and ψ and λ were more similar between the species. Reach 3 (North Canal Dam to Benham Falls) was the only area in which Redband Trout showed higher relative abundance than Brown Trout. These reach-level status estimates provide spatial information needed to identify and prioritize management actions to improve status and a baseline from which to track population response to changes in environmental conditions and riverine management.

It is not clear which factors may be limiting the occupancy and abundance of Redband Trout in the upper two reaches of the Deschutes River. Given the dramatic alterations to the river in these reaches, there may be many potential confounding factors. These factors include inter- and intra-specific interactions, water temperature, habitat fragmentation, and the managed discharge regime. Redband trout were sympatric with Brown Trout, Mountain Whitefish, and hatchery-raised Rainbow Trout and Redband Trout. Although relatively high occupancy and abundance of Brown Trout did not result in competitive exclusion of Redband Trout, this pattern may be expected for a number of reasons. Brown Trout have high overlap in food and habitat use with other trout species (Gatz et al. 1987; McHugh et al. 2006) and they are more aggressive at similar sizes, even when smaller than other trout (Fausch and White 1981; Shirvell and Dungey 1983; Wang and White 1994; McHugh and Budy 2005). When in sympatry with Brown Trout, some trout species shifted to less preferred habitat (Gatz et al. 1987; Wang and White 1994), changed dietary habits (McHugh and Budy 2006), and displayed worse performance, such as consumption of smaller prey, slower growth, and worse condition (McHugh and Budy 2005). Although this information comes from studies conducted in experimental channels or small streams (i.e., 3rd and 4th order), it suggests that competition with Brown Trout may be one of the factors limiting growth and relative abundance of Redband Trout in the upper Deschutes River.

Mountain Whitefish was the dominant salmonid species throughout this study area, which is common when this species and Redband Trout occur in sympatry in this region (Gray 1986, Whitman 2002, WPN 2002). Mountain Whitefish removal programs have been conducted in the Deschutes River basin (e.g., Odell Creek, Fies et al. 1996) and in other areas of the western United States (Meyer et al. 2009) because of the unsubstantiated perception that they limited trout production through competition for food and habitat. However, diet studies show that although there may be some dietary overlap between Mountain Whitefish and Redband Trout, the two species generally partition the habitat, with Mountain Whitefish tending to feed on benthic invertebrates and Redband Trout tending to feed more on terrestrial insects on the water surface and invertebrates drifting within the water column (McHugh 1940, Fuller 1981, Pontius and Parker 1973, Dos Santos 1985). This suggests that Mountain Whitefish are unlikely to be a limiting factor for Redband Trout.

The majority of the large Redband Trout captured in reaches 4 and 5 were adipose fin-clipped hatchery fish. Annual stocking of hatchery fish appeared to be accomplishing its intended effect of providing fish for a put-and-take recreational fishing opportunity, but there could also be unintended effects. For example, these large size-class hatchery fish may reduce the native population size through intra-specific competition and predation. Genetic studies, such as in the upper Snake River basin in Idaho (Kozfkay et al. 2011) and the Metolius River in Oregon (Currens et al. 1997, Williams et al. 1997) have demonstrated that hybridization can occur when coastal Rainbow Trout are stocked in areas where native inland Redband Trout occur. Native salmonid populations have better fitness than their hatchery-raised counterparts (Araki et al. 2009, Christie et al. 2014) because they have adapted to local environmental conditions (Allendorf and Leary 1986, Currens et al. 1997). One case study within the Deschutes River basin showed that the end of a hatchery stocking program coincided with a subsequent increase in abundance of the native Redband Trout population (see Riehle and Dachtler 2011). Given that the status of native Redband Trout is relatively poor in the same two upper reaches in which hatchery fish are stocked and hybridization between wild and hatchery Redband Trout has been observed (Bohling et al.

2017), more research is needed to determine the influence of hatchery-raised fish on native Redband Trout in these reaches.

The influence of dams on fish populations and riverine ecosystems has been widely documented (see Bednarek 2001). The hydrologic regime in this study area has been dramatically altered by the construction of storage dams and water management mainly for irrigation and other human activities (Golden and Alyward 2006) and with little consideration for the seasonal habitat requirements of Redband Trout and other native aquatic species. At the end of the irrigation season in October, Wickiup Dam dramatically reduces discharge in the upper segment to refill its reservoir. Low winter discharge reduces habitat volume for overwintering fish in this segment and likely reduces the aquatic prey base (Dimick et al. 1947). Wickiup Dam directly blocks upstream migratory access to historical spawning areas for native fishes and alters downstream habitat by restricting wood and sediment transport needed for formation of spawning habitat and channel complexity (e.g., islands and gravel bars). The loss of access to historical spawning areas has likely reduced migratory fish abundance in the two river reaches downstream of Wickiup Dam. More research is needed to understand how low winter discharge and impeding the supply of sediment and wood at Wickiup Dam have affected habitat complexity, food availability, and Redband Trout status downstream of the dam.

The managed discharge regime may differentially affect spring-spawning Redband Trout and fallspawning Brown Trout and Mountain Whitefish. Redband Trout in the middle and upper Deschutes River spawn April through June (NPCC 2004); although spawning has been observed in the lower Deschutes River from March to August (Zimmerman and Reeves 1999). Under the current flow management regime in the upper segment, Redband Trout spawning begins as river discharge increases rapidly and then continues with relative instability throughout the spawning and egg incubation period. Thus, Redband Trout eggs and alevins developing in the redd are exposed to several large discharge fluctuations and may be harmed by changing interstitial flow dynamics or dewatering. Under the managed discharge regime in the middle segment of the Deschutes River, discharge drops dramatically in April when the irrigation season starts and is then held relatively constant during the Redband Trout spawning and egg incubation period.

It is not clear how the altered hydrologic regime impacts the Brown Trout life cycle. Brown Trout spawn in October and November, generally when flows are at their lowest, and fry emerge in March (Fies et al. 1996), just as managed flows start rapidly increasing. Autumn low discharge appeared to be more stable than spring and summer high discharge. Although low discharge may reduce available spawning habitat, more stable discharge may also reduce the risk of harm to redds. It is also possible that Brown Trout fry have access to relatively more rearing habitat throughout the spring and summer high discharge period and experience relatively greater dispersal. Furthermore, Brown Trout fry are larger and possess greater swimming ability than Redband Trout fry during the rapid transition to low flows and, as a result, may have better survival during this period. Mountain Whitefish, in contrast to the trout species, are broadcast spawners and have different spawning habitat requirements. This study shows that Mountain Whitefish do not appear to be limited in these upper reaches by Wickiup Dam and the managed flow regime. However, more research is required to understand how the current managed flow affects the spawning habitat and recruitment of Redband Trout and Brown Trout.

Conclusions

The extra time and cost required and often unreliable estimates produced by sampling designs with abundance estimators have led some to suggest shifting the focus of status assessment and monitoring to species occupancy (MacKenzie et al. 2006, Couturier et al. 2013). Even with the small sample size of this study, the occupancy sampling design produced reliable estimates. If this sampling design is implemented in the future, there are recommendations for reducing sampling effort that do not compromise estimator reliability (MacKenzie et al. 2006) and multi-state occupancy models that can incorporate different lifestages or levels of abundance (Nichols et al. 2007). Further bolstering this advice, this study found that N-mixture and closed capture sampling designs provided imprecise and potentially biased abundance estimates in this study. Increasing sampling effort, sample size, and site length as well as incorporating additional fish capture methods would likely improve the accuracy of the abundance estimates; however, rather than guaranteeing a reliable sampling design for tracking trend in status, it would only guarantee increased costs and reduced affordability for finite monitoring budgets. Given this difficulty with traditional abundance sampling designs and acknowledging that abundance estimation is often desired for management purposes, managers in this study area should consider evaluating sampling designs using genetic assessment sampling designs that have been shown to produce reliable estimates of effective population size and effective number of breeders of trout, salmon, and other animals (e.g., Waples and Do 2010, Whiteley et al 2011, Allendorf et al. 2013).

References

Allendorf, F.W., and R.F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. Conservation biology: the science of scarcity and diversity. M.E. Soule, editor. Sinauer Associates Inc., 584 p. 57-76.

Allendorf, F.W., G. Luikart, and S.N. Aitken. 2013. Conservation and the genetics of populations. In 2nd edition. Wiley-Blackwell, Chichester.

Araki, H., B. Cooper, and M. S. Blouin 2009. Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. Biology Letters 5:621–624.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74: 1175-1178. DOI: 10.2193/2009-367

Bednarek, A. T. 2001. Undamming rivers: a review of the ecological impacts of dam removal. Environmental Management 27:803–814.

Bohling, J., J. Von Bargen, and S. Starcevich. 2017. Evaluation of genetic population structure and effective population size among populations of Redband Trout in the Deschutes River, OR. Abernathy Fish Technology Center, US Fish and Wildlife Service, Longview, WA. Final report.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY.

Christie, M. R., M. J. Ford, and M. S. Blouin. 2014. On the reproductive success of early-generation hatchery fish in the wild. Evolutionary Applications 7: 883-896. DOI:10.1111/eva.12183.

Conroy, M. J., and Carroll, J. P. (2009). Quantitative conservation of vertebrates. Chichester, West Sussex, UK: Wiley-Blackwell.

Couturier, T., M. Cheylan, A. Bertolero, G. Astruc, and A. Besnard. 2013. Estimating abundance and population trends when detection is low and highly variable: A comparison of three methods for the Hermann's tortoise. The Journal of Wildlife Management, 77: 454-462. DOI:10.1002/jwmg.499.

Currens, K. P., A. R. Hemmingsen, and R. A. French. 1997. Introgression and susceptibility to disease in a wild population of Rainbow Trout. North American Journal of Fisheries Management 17:1065–1078.

Dimick, J. B., and C. J. Campbell. 1947. Recommended minimum flows below Wickiup Reservoir. Oregon State Game Commission Report.

DosSantos, J. M. 1985. Comparative food habits and habitat selection of Mountain Whitefish and Rainbow Trout in the Kootenai River, Montana. Master's thesis. Montana State University, Bozeman.

Efford, M. G., and D. K. Dawson. 2009. Effect of distance-related heterogeneity on population size estimates from point counts. The Auk 126(1):100-111. DOI:10.1525/auk.2009.07197.

Fausch, K. D., and R. J. White. 1981. Competition between Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220–1227.

Fies, T., J. Fortune, B. Lewis, M. Manion, and S. Marx. 1996. Upper Deschutes River subbasin fish management plan. Bend, Oregon.

Fiske, I., and R. Chandler (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43: 1-23.

Fuller, R. K. 1981. Habitat utilization, invertebrate consumption, and movement by salmonid fishes under fluctuating flow conditions in the Big Lost River, Idaho. Master's thesis. Idaho State University, Pocatello.

Gannett, M. W., M. Manga, and K. E. Lite Jr. 2003. Groundwater hydrology of the upper Deschutes Basin and its influence on streamflow. Water Resources and Application 7:31–70.

Gatz, A. J., M. J. Sale, and J. M. Loar. 1987. International association for ecology habitat shifts in Rainbow Trout: competitive influences of Brown Trout. Oecologia 74:7–19.

Gerrodette, T. (1993). Program Trends: User's Guide. NOAA, Southwest Fisheries Science Center.

Golden, B., and B. Aylward. 2006. Instream flow in the Deschutes Basin: monitoring, status and restoration needs. Deschutes Water Alliance Final Report. Bend, Oregon.

Grabowski, T. B., T. D. Ferguson, J. T. Peterson, and C. A. Jennings. 2009. Capture probability and behavioral response of the Robust Redhorse, a cryptic riverine fish, to electrofishing. North American Journal of Fisheries Management 29: 721-729. DOI: 10.1577/M08-060.1.

Gray, E. 1986. Roughing it on the Little Deschutes River 1934-1944: A history of a sawmill camp and its people. K & M Printing and Lithographing, Inc., Eugene, Oregon.

Gwinn, D. C., P. Brown, J. C. Tetzlaff, and M. S. Allen. 2011. Evaluating mark - recapture sampling designs for fish in an open riverine system. Marine and Freshwater Research 62:835-840.

Harper, C. K., Bromaghin, J. F., & Klosiewski, S. P. (2005). Rainbow Trout abundance in the Kisaralik River, Yukon Delta National Wildlife Refuge, Alaska, 1997. Alaska Fisheries Technical Report Number 78.

IPCC (Intergovernmental Panel on Climate Change). 2014. Climate Change 2014: Synthesis Report. Contribution of working groups I, II, and III to the fifth assessment report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pages.

Jacobsen, R.L. and S. Jacobs. 2010. Evaluation of raft electrofishing for fish sampling in the Middle Deschutes River. Oregon Department of Fish and Wildlife, Native Fish Investigations Project, Corvallis, Oregon.

Kéry M., and J. A. Royle. (2016) Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS. 1st Edition. Academic Press & Elsevier. 808 pages.

Kozfkay, C. C., M. R. Campbell, K. A. Meyer, and D. J. Schill. 2011. Influences of habitat and hybridization on the genetic structure of Redband Trout in the upper Snake River Basin, Idaho. Transactions of the American Fisheries Society 140:282–295.

Laake, J.L. (2013). RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle, WA.

Lee, C. D. 2013. Redband Trout spawning and fry emergence study: Abundance and year class strength component. Avista Corporation and USEPA Bonneville Power Administration. Spokane, Washington, pp. 22.

Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Ecological effects downstream of dams: a geomorphic perspective. BioScience 45:183–192.

MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology, 84: 2200-2207. DOI: 10.1890/02-3090.

MacKenzie, D.I., and L. L. Bailey. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9: 300-318. DOI: 10.1198/108571104X3361.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier Inc., Burlington MA.

Mazerolle, M. J. 2017. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 3.4.3.

McHugh, J. L. 1940. Food of the Rocky Mountain Whitefish *Prosopium williamsoni*. Journal of the Fisheries Research Board of Canada 5:131–137.

McHugh, P., and P. Budy. 2005. An experimental evaluation of competitive and thermal effects on Brown Trout (*Salmo trutta*) and Bonneville cutthroat Trout (*Oncorhynchus clarkii utah*) performance along an altitudinal gradient. Canadian Journal of Fisheries and Aquatic Sciences 62:2784–2795.

McHugh, P., and P. Budy. 2006. Experimental effects of nonnative Brown Trout on the individual- and population-level performance of native Bonneville Cutthroat Trout. Transactions of the American Fisheries Society 135:1441–1455.

Meyer, K. A., F. S. Elle, and J. A. Lamansky. 2009. Environmental factors related to the distribution, abundance, and life history characteristics of Mountain Whitefish in Idaho. North American Journal of Fisheries Management 29:753–767. DOI:10.1577/M08-015.1

Muhlfeld, C. C., Bennett, D. H., & Marotz, B. (2001). Summer habitat use by Columbia River Redband Trout in the Kootenai River Drainage. North American Journal of Fisheries Management 21: 223–235. DOI: 10.1577/15488675(2001)021<0223:SHUBCR>2.0.CO;2.

Newton, D., M. Perle, and J. Polvi. 2006. Future ground water demand in the Deschutes basin. Deschutes Water Alliance Issue Paper – Final Report. Redmond, OR.

Nichols, J. D., J. E. Hines, D. I. Mackenzie, M. E. Seamans, and R. J. Gutierrez. 2007. Occupancy estimation and modeling with multiple states and state uncertainty. Ecology 88:1395–1400.

Nuhfer, A. J. 1988. A Comparison of Growth of Brown Trout from Selected Western Rivers with Growth of Brown Trout from Michigan Rivers. Fisheries Technical Report No. 88-6, MI.

NPCC (Northwest Power Planning Council). 2004. Deschutes Subbasin Plan. Northwest Power Planning Council. Portland, Oregon.

Odenkirk, J., and S. Smith (2005). Single- versus multiple-pass boat electrofishing for assessing Smallmouth Bass populations in Virginia rivers. North American Journal of Fisheries Management 25: 717–724. DOI:10.1577/M04-067.1.

Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. Wildlife Monographs, 62, 3–135.

Pettit, S. W., and R. L. Wallace. 1975. Age, growth, and movement of Mountain Whitefish, *Prosopium williamsoni* (Girard), in the North Fork Clearwater River, Idaho. Transactions of the American Fisheries Society 104:68–76.

Pine, W.E., K.H. Pollock , J.E. Hightower , T. J. Kwak, and J.A. Rice. 2003. A review of tagging methods for estimating fish population size and components of mortality. Fisheries 28:10-23. DOI: 10.1577/1548-8446(2003)28 [10:AROTMF]2.0.CO;2.

Pontius, R. W., and M. Parker. 1973. Food habits of the Mountain Whitefish, *Prosopium williamsoni* (Girard). Transactions of the American Fisheries Society 102:764–773.

PRC (Population Research Center). 2015. Coordinated population forecast for Deschutes County, its urban growth boundaries (UGB), and area outside UGBs: 2015-2065. College of Urban and Public Affairs, Portland State University. Portland, OR.

R Core Team. 2017. A language and environment for statistical computing. Vienna, Austria. URL: https://www.R-project.org/.

Riehle, M., and N. Dachtler. 2011. Redband Trout (*Oncorhynchus mykiss*) spawning surveys in the upper Metolius River, Oregon, 2009-2010. Item 11b in Pelton Rounde Butte 2011 Fisheries Workshop DVD.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–15.

Saunders, W. C., Budy, P. and Thiede, G. P. (2015), Demographic changes following mechanical removal of exotic Brown Trout in an Intermountain West (USA), high-elevation stream. Ecology of Freshwater Fish 24: 252-263. DOI:10.1111/eff.12143.

Schroeder, K. R. and L.H. Smith. 1989. Life history of Rainbow Trout and effects of angling regulations, Deschutes River, Oregon. Information Report Number 89-6. Oregon Department of Fish and Wildlife. Salem, Oregon.

Shirvell, C. S., and R. G. Dungey. 1983. Microhabitats chosen by Brown Trout for feeding and spawning in rivers. Transaction of the American Fisheries Society 112:355–367.

Wang, L., and R. J. White. 1994. Competition between wild Brown Trout and hatchery Greenback Cutthroat Trout of largely wild parentage. North American Journal of Fisheries Management 14:475–487.

Waples, R.S., and Do, C. 2010. Linkage disequilibrium estimates of contemporary N e using highly variable genetic markers: a largely untapped resource for applied conservation and evolution. Evolutionary Applications 3: 244–262. DOI: 10.1111/j.1752-4571.2009.00104.x.

Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change.Proceedings of the National Academy of Sciences of the United States of America 108:14175–14180.

Whiteley, A.R., J. A. Coombs, M. Hudy, Z. Robinson, K.H. Nislow, and B.H. Letcher. 2012. Sampling strategies for estimating Brook Trout effective population size. Conservation Genetics 13: 625–637. DOI: 10.1007/s10592-011-0313-y.

Whitman, T. 2002. Crooked River watershed assessment. Prineville, Oregon.

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

Williams, R. N., R. F. Leary, and K. P. Currens. 1997. Localized genetic effects of a long-term hatchery stocking program on resident Rainbow Trout in the Metolius River, Oregon. North American Journal of Fisheries Management 14:1079–1093.

WPN 2002. Little Deschutes River Subbasin assessment. Watershed Professionals Network, Boise, Idaho.

Zimmerman, C.E. and G.H. Reeves. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 57:2152-2162.