Transactions of the American Fisheries Society 143:899–909, 2014
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ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2014.901248

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ARTICLE

Relationship between Juvenile Fish Condition and Survival to Adulthood in Steelhead

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Abstract

Understanding how individual characteristics are associated with survival is important to programs aimed at recovering fish populations of conservation concern. To evaluate whether individual fish characteristics observed during the juvenile life stage were associated with the probability of returning as an adult, juvenile steelhead *Oncorhynchus mykiss* from two distinct population segments (DPSs; Snake River and upper Columbia River) were captured, photographed to determine external condition (body injuries, descaling, signs of disease, fin damage, and ectoparasites), measured, classified by rearing type (hatchery, wild), marked with a PIT tag, and released to continue out-migration to the Pacific Ocean during 2007–2010. The PIT tags of returning adults were interrogated in fishways at hydroelectric dams on the lower Columbia River 1–3 years following release as juveniles. Juvenile-to-adult survival models were investigated independently for each DPS and indicated that similar individual fish characteristics were important predictors of survival to adulthood for both steelhead populations. The data analysis provided strong support for survival models that included explanatory variables for fish length, rearing type, and external condition, in addition to out-migration year and timing. The probability of a juvenile surviving to adulthood was positively related to length and was higher for wild fish compared with hatchery fish. Survival was lower for juveniles with body injuries, fin damage, and external signs of disease. Models that included variables for descaling and ectoparasite infestation, however, had less support than those that incorporated measures of body injuries, fin damage, and disease. Overall, results indicated that individual fish characteristics recorded during the juvenile life stage can be used to predict adult survivorship in multiple steelhead populations.

Agencies involved in the recovery of populations of Pacific salmonids *Oncorhynchus* spp. in the Columbia River basin that are listed under the U.S. Endangered Species Act (ESA) have dedicated substantial resources to increase salmonid survival. For instance, hydroelectric dams and operations have been modified to increase fish passage efficiency, decrease travel times, and reduce direct injury resulting from passage (Johnson et al. 2000; Ferguson et al. 2007). Efforts to restore or enhance stream habitats have been implemented (NPCC 2013) and hatcheries have been used to bolster juvenile fish production and supplement wild populations (CBFWA 1990). As part of these recovery efforts, monitoring programs have been implemented to record data on the external condition, size, rearing type (hatchery, wild), and other biological metrics of out-migrating juvenile

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Received August 20, 2013; accepted February 14, 2014

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salmonids (FPC 2012). Despite these extensive efforts, evaluations of the influence of individual juvenile fish characteristics (e.g., length, rearing type, and external condition) on survival to adulthood are generally lacking, but may be paramount in the identification of factors that influence survival between multiple life stages (Zabel and Achord 2004).

Individual fish characteristics measured during juvenile salmonid out-migration have been linked to a host of juvenile performance metrics in the Columbia River basin (Zabel and Achord 2004; Zabel et al. 2005; Hostetter et al. 2011, 2012; Connon et al. 2012). Fork length of juvenile salmonids has been associated with juvenile survival in multiple populations of salmonids (Zabel and Achord 2004; Zabel et al. 2005). Rapid, nondestructive techniques used to examine juvenile fish have linked external lesions and disease symptoms to increased susceptibility to predation and decreased juvenile survival in Snake River steelhead *O. mykiss* (Hostetter et al. 2011, 2012). Together these studies indicate that juvenile salmonids vary in their physical attributes and health status, and this variation is associated with differences in juvenile survival during out-migration.

Environmental conditions experienced during the juvenile life stage are known to influence survival to adulthood in salmonids (Scheuerell et al. 2009; Petrosky and Schaller 2010; Haeseker et al. 2012). To date, juvenile-to-adult survival studies have primarily focused on population-level variables (i.e., variables that affect groups of fish), linking environmental conditions such as out-migration timing to survival probabilities (Scheuerell et al. 2009; Petrosky and Schaller 2010). Population-level analyses provide valuable insight into trends that affect groups of fish, but assume individual variation within those groups is negligible (Juanes et al. 2000). Survival is a process at the individual level, however, and evaluation of individual characteristics can provide valuable insight for fish recovery plans and strategies, especially if the variables that influence survival are subject to management control.

In the present study, data on the characteristics of individual juvenile fish were collected along with population-level data for two distinct population segments (DPSs; Waples 1991) of steelhead in the Columbia River basin: Snake River steelhead and upper Columbia River steelhead. The primary goals of the study were to (1) investigate the influence of individual-level fish characteristics on juvenile-to-adult survival and (2) determine whether results were consistent across two DPSs of steelhead. This study also provides the first attempt to validate rapid, nondestructive, external examination techniques (Hostetter et al. 2011) as survival performance metrics on multiple salmonid populations, between multiple life stages.

METHODS

Study site.—Our research efforts focused on out-migrating juvenile steelhead from two DPSs: Snake River (SR) steelhead and upper Columbia River (UCR) steelhead. Snake River steelhead were collected at juvenile collection facilities at either Lower Monumental Dam (river kilometer [rkm] 589) or Ice Harbor Dam (rkm 538) on the lower Snake River, Washington (Figure 1). Upper Columbia River steelhead were captured at the juvenile collection facility at Rock Island Dam (rkm 729) on the Columbia River, Washington (Figure 1). Juveniles of both steelhead DPSs migrate to the Pacific Ocean during the smolt life stage. Once in the ocean, UCR steelhead mature in 1–2 years before returning to the river to spawn and SR steelhead mature in 1–3 years before returning to spawn (Busby et al. 1996).

Juvenile capture, tagging, and examination.—Individual fish characteristics selected for inclusion in the study were identified by Hostetter et al. (2011) as possible survival performance metrics in juvenile steelhead. Methods for capture, tagging, and release of juvenile SR steelhead were thoroughly described in Hostetter et al. (2011). Methods of capture, tagging, and examination of juvenile UCR steelhead were identical to those for SR steelhead, except that juvenile UCR steelhead were collected at Rock Island Dam (Figure 1). Juvenile SR steelhead were captured and released during 2007–2009, while juvenile UCR steelhead were captured and released during 2008–2010.

Rapid, noninvasive examination techniques are those of Hostetter et al. (2011) and are briefly summarized here. Juvenile steelhead were anesthetized with tricaine methanesulfonate (MS-222) and tagged with a 12-mm (length) × 2-mm (width) PIT tag (134.2 kHz) via a modified hypodermic syringe equipped with a 12-gauge needle (Prentice et al. 1990a, 1990b; Nielson 1992). After a steelhead was PIT-tagged, it was placed in a watered sample tray, measured (FL, nearest centimeter), classified by rearing type (wild: indicated by the presence of fully intact fins; hatchery: indicated by the absence of an adipose fin or by characteristics associated with hatchery rearing practices, including the removal or erosion of pectoral, pelvic, or dorsal fins), and digitally photographed (Canon EOS Rebel XTi camera; Canon EF 50-mmf/2.5 Compact Macro lens; Bencher Copymate II copy stand with fluorescent light source). Digital photographs were taken of both sides of each fish. Total handling time for each fish was <30 s. Detailed information on the external condition of each steelhead (i.e., body injuries, descaling, external signs of disease, fin damage, and ectoparasite infestations) were collected by analyzing the digital photographs (see Table 1 for a full description of condition scoring). Equal tagging effects among fish by DPS, condition type, size, and rearing type were assumed.

Juvenile steelhead were sampled in proportion to the numbers captured at each dam during each of three time periods. Time periods were then used as a measure of out-migration timing based on when the first 10% (early), middle 80% (peak), and last 10% (late) of the out-migrating juvenile steelhead population passed the collection dam each year per Hostetter et al. (2011). Hence, each individually PIT-tagged juvenile steelhead used in the study was assigned values for DPS, out-migration year, out-migration timing, rearing type, FL, and each of the five external condition categories evaluated.

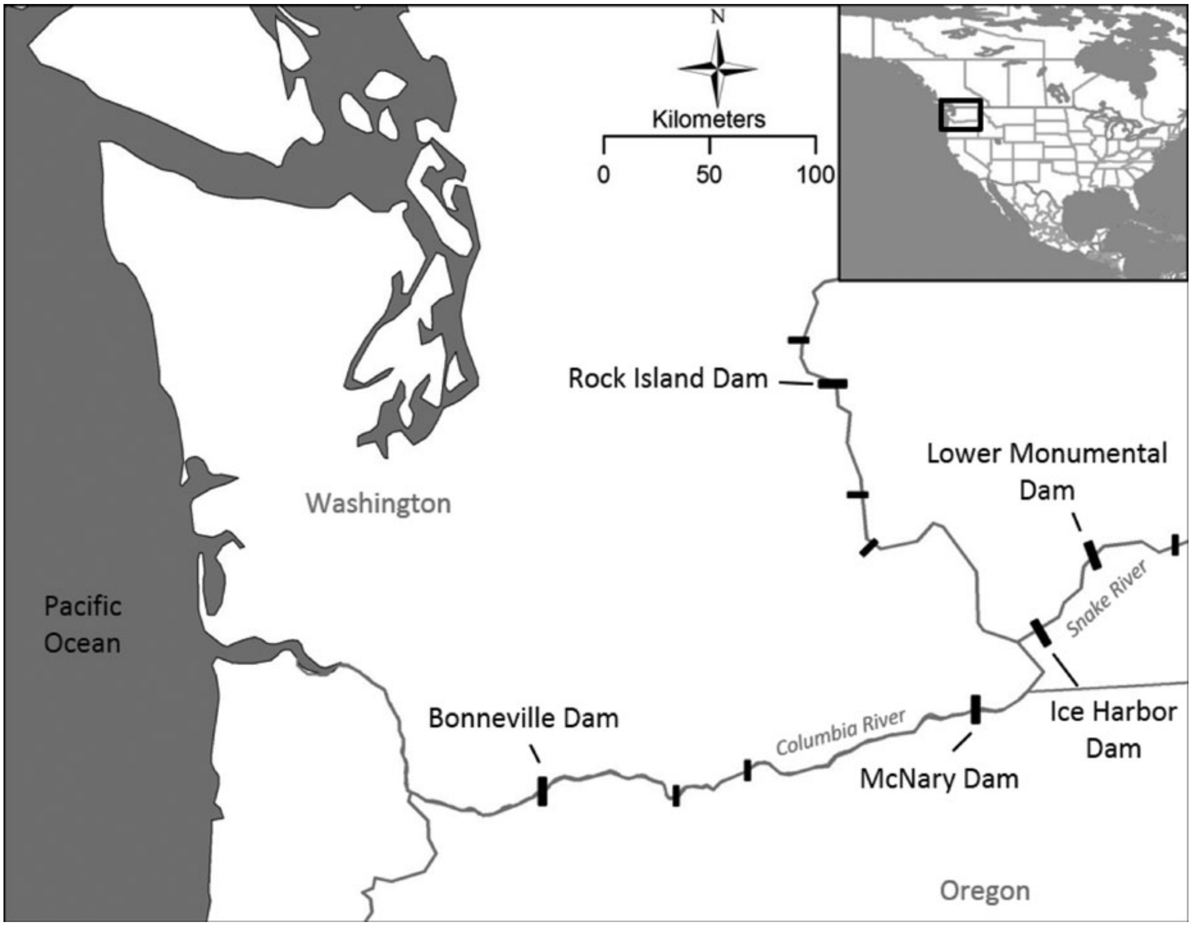

FIGURE 1. The main-stem Snake and Columbia rivers with major hydroelectric dams denoted by bars. Juvenile steelhead PIT-tagged and released from Lower Monumental, Ice Harbor, or Rock Island dams were detected as returning adults at Bonneville and McNary dams.

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Adult returns.—An individual juvenile steelhead was considered to have returned as an adult if its PIT tag was detected passing an adult fishway or ladder at Bonneville Dam (rkm 234) or McNary Dam (rkm 470) within 1 to 2 years (UCR steelhead) or 1 to 3 years (SR steelhead) following tagging and release as a juvenile (Busby et al. 1996; Scheuerell et al. 2009; Figure 1). Following the methods described by Keefer et al. (2008) and based on information that detection probabilities of adult salmonids at Bonneville Dam are extremely close to 1.0 (Tenney et al. 2010), the resulting juvenile-to-adult return rates are accurate but should be considered an index due to the possibility that an adult not detected at Bonneville Dam could die before reaching McNary Dam. Adult interrogation data were retrieved from the PIT Tag Information System (www.ptagis.org; accessed February 2013) maintained by the Pacific States Marine Fisheries Commission (Gladstone, Oregon). In total, the SR steelhead data set consisted of 29,959 PIT-tagged juveniles and 443 returning adults (Table 2). The UCR steelhead data set consisted of 21,739 PIT-tagged juveniles and 385 returning adults (Table 2).

Statistical analyses.—Variation in juvenile-to-adult survival was investigated using mark–recapture data for individually PIT-tagged juvenile steelhead. Individual steelhead were assigned a value of 1 if they were detected in the Bonneville or McNary dam fishway as an adult or a value of 0 if they were not detected and were presumed dead. Logistic regression (Hosmer and Lemeshow 2000) and model selection (Burnham and Anderson 2002) were used to determine whether juvenile survival to adulthood was associated with explanatory variables recorded during the juvenile life stage.

To evaluate the importance of individual-level and population-level data on survival to adulthood, we compared survival models that included only population-level variables with models that included both population-level variables and individual-level variables. This was accomplished by evaluating whether the inclusion of individual-level data (FL, rearing type, or external condition) created more parsimonious models relative to models that only incorporated population-level data (out-migration year [hereafter "year"] and out-migration timing [hereafter "timing"]). Population-level variables of year

TABLE 1. Individual fish characteristic descriptions and presence for juvenile steelhead captured and marked with a PIT tag at Lower Monumental or Ice Harbor dams on the Snake River (SR) during 2007–2009 ($n = 29{,}959$) and Rock Island Dam on the upper Columbia River (UCR) during 2008–2010 ($n = 21{,}739$). External condition descriptions are from Hostetter et al. (2011).

Individual characteristic	Number tagged (% per characteristic) SR	Number tagged (% per characteristic) UCR	Description
Body injury			
Absent	21,007 (80.9%)	18,013 (82.9%)	No visible hemorrhages, scars, or other damage to the head, trunk, operculum, or eyes.
Moderate	3,027 (11.7%)	2,832 (13.0%)	Closed or healed scars to the head, trunk, operculum, or eyes
Severe	1,925 (7.4%)	894 (4.1%)	Deformity, open wound, or large surface area scars on head, trunk, operculum, or eyes
Descaling			
<5%	17,014 (65.5%)	17,363 (79.9%)	Scale loss on <5% of body
5–20%	7,925 (30.5%)	4,009 (18.4%)	Scale loss on 5–20% of body
>20%	1,020 (3.9%)	367 (1.7%)	Scale loss on >20% of body
Disease			
Absent	24,967 (96.2%)	21,256 (97.8%)	No external symptoms of bacterial, fungal, or viral infections
Moderate	349 (1.3%)	163 (0.7%)	Visible infection limited to one external area
Severe	643 (2.5%)	320 (1.5%)	Visible infection in multiple areas or symptoms that suggest a systemic infection
Ectoparasites			
Absent	25,252 (97.3%)	20,597 (94.7%)	No visible ectoparasites
Moderate	531 (2.0%)	877 (4.0%)	Visible ectoparasites found in one area
Severe	176 (0.7%)	265 (1.2%)	Visible ectoparasites in more than area or on gills
Fin damage			
Absent	5,792 (22.3%)	10,148 (46.7%)	Fin wear and damage < 50% on any fin
Moderate	14,571 (56.1%)	11,121 (51.2%)	Fin wear and damage > 50% on one or two fins
Severe	5,596 (21.6%)	470 (2.2%)	Fin wear and damage > 50% on three or more fins
Rearing type			
Wild	3,808 (14.7%)	5,836 (26.8%)	Presence of an adipose fin and minimal fin erosion
Hatchery	22,151 (85.3%)	15,903 (73.2%)	Absence of an adipose fin or other characteristics associated with hatchery rearing practices, including the erosion of pectoral, pelvic, caudal, or dorsal fins
FL	22.0 (3.2) cm	19.6 (2.5) cm	Mean (SD) FL in centimeters

and timing were previously documented to influence survival of juvenile salmonids to adulthood (Sandford and Smith 2002; Scheuerell et al. 2009; Petrosky and Schaller 2010) and therefore were included in every model except the null model. Models were evaluated separately for each steelhead DPS to provide independent validation of results across two steelhead populations.

The Hosmer–Lemeshow goodness-of-fit test was evaluated using the most parameterized additive model for each DPS. Models were ranked by Akaike's information criterion corrected for small sample size (AIC_c) and Akaike weights ($\mathrm{AIC}_c\ w$; Burnham and Anderson 2002). Model-averaged parameter estimates were used to evaluate the effect of each variable on juvenile-to-adult survival and produce a more honest measure of precision for each parameter estimate (Burnham and Anderson 2002). Model-averaged parameter estimates were calculated from the 95% confidence set of models using the natural average of the estimates (Burnham and Anderson 2002). Model-averaged coefficients were back-transformed to describe the relative odds of an event occurring at various levels of a covariate after accounting for the other variables in the model (i.e., odds ratio: Hosmer and Lemeshow 2000). To further examine the influence of individual-level variables on variation in adult return rates, fitted survival rates from model-averaged coefficients were compared with the minimum and average juvenile-to-adult (also referred to as smolt-to-adult) management survival goals of 2% and 4%, respectively, for SR steelhead and UCR steelhead (NPCC 2009).

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TABLE 2. The number of steelhead captured and marked as juveniles (Released) and subsequently detected as returning adults (Returned). Juvenile steelhead were marked with a PIT tag at Lower Monumental or Ice Harbor dams on the Snake River (SR; 2007–2009) and at Rock Island Dam on the upper Columbia River (UCR; 2008–2010).

	SR			UCR		
Year	Released	Returned	%	Released	Returned	%
2007	7,085	41	0.6			
2008	9,173	297	3.2	7,266	219	3.0
2009	9,701	105	1.1	7,109	78	1.1
2010				7,364	88	1.2
Total	25,959	443	1.7	21,739	385	1.8

All analyses were conducted using R statistical software version 2.15.3 (R Core Development Team 2013), specifically the glm function for logistic regression, package AICcmodavg for model-averaged parameter estimates, and the cor function to investigate collinearity among external conditions via the Pearson's correlation coefficients (r) prior to analyses.

RESULTS

In total, 129 models were tested for each steelhead DPS. Hosmer–Lemeshow goodness-of-fit tests provided no evidence for a lack of fit in the global models ($P = 0.20$ and 0.57 for SR steelhead and UCR steelhead, respectively). Pearson's correlation coefficients indicated minimal correlation among external conditions ($|r| < 0.16$ and < 0.25 for SR steelhead and UCR steelhead, respectively). Based on AIC$_c$ rankings, survival models that included individual fish characteristic variables for length, rearing type, body injuries, disease symptoms, and fin damage, as well as the population level variables for year and out-migration timing were consistently selected as top models. Results for SR steelhead and UCR steelhead indicated that both population-level variables (year and timing) and individual-level variables (length, rearing type, and external condition) recorded during the juvenile life stage were important factors in predicting the probability of survival to adulthood (Table 3). Support for these variables was consistent across both the SR steelhead and UCR steelhead DPSs (Table 3). Survival models that only included population-level variables (year and timing) had little support relative to models that also included individual fish characteristics for either steelhead DPS (Table 3).

External condition variables recorded during the juvenile life stage were important factors in predicting the probability of a juvenile steelhead surviving to adulthood in both steelhead DPSs (Table 3). Top models predicting survival of SR steelhead consistently included external condition variables for body injuries and external disease symptoms, and often included the variable for fin damage (Tables 3, A.1 in the Appendix). Similar trends were observed for UCR steelhead, where top models predicting survival always included variables for external disease symptoms and fin damage, and often included the variable for body injuries (Tables 3, A.1). Overall, data indicated that body injuries, disease symptoms, and fin damage were the best-supported condition metrics across steelhead DPSs (Table 3). The influence of other external condition variables (i.e., descaling and ectoparasites) on juvenile-to-adult survival, however, was less supported and often not consistent between steelhead DPSs (Table A.1).

Survival of juvenile steelhead to adulthood was often lower for individuals with body injuries, fin damage, and external signs of disease relative to juvenile steelhead that did not display these conditions (Table 4). The average magnitude of each condition estimate was similar between the two steelhead DPSs (Table 4). Snake River steelhead and UCR steelhead without external disease symptoms were 3.7 times (95% CI, 0.9–14.9)

TABLE 3. Relative performance of top candidate models predicting juvenile survival to adulthood for Snake River steelhead and upper Columbia River steelhead. Variables are year (Y), out-migration timing (T), fork length (L), rearing type (REAR), body injuries (BODY), external symptoms of disease (DISEASE), and fin damage (FIN); see Table 1 for variable descriptions. K is the number of parameters, ΔAIC$_c$ is the difference in AIC$_c$ between the top-ranked model and the model of interest, and AIC$_c$ weights (AIC$_c$ w) give relative support for any particular model. Models with $\Delta\text{AIC}_c < 2.0$, the best model without individual fish characteristics (Y + T), and the null model are shown (see Table A.1 for results of all models with AIC$_c$ $w > 0.01$.

Model	K	AIC$_c$	ΔAIC$_c$	AIC$_c$ w
Snake River steelhead				
Y + T + L + DISEASE + BODY + REAR	11	4,161.58	0.00	0.30
Y + T + L + DISEASE + BODY + REAR + FIN	13	4,161.92	0.34	0.25
Y + T	5	4,261.84	100.26	0.00
Null	1	4,487.04	325.46	0.00
Upper Columbia River steelhead				
Y + T + L + DISEASE + FIN + REAR	11	3,640.88	0.00	0.24
Y + T + L + DISEASE + FIN	10	3,642.23	1.35	0.12
Y + T + L + DISEASE + FIN + REAR + BODY	13	3,642.30	1.43	0.12
Y + T	5	3,685.45	44.57	0.00
Null	1	3,871.03	230.15	0.00

TABLE 4. Model-averaged parameter estimates and odds ratios (95% confidence limits) for the best supported variables used to predict juvenile-to-adult survival of Snake River steelhead (SR) and upper Columbia River steelhead (UCR). Parameter confidence intervals that did not overlap zero are denoted by an asterisk.

	SR		UCR	
Variable	Parameter	Odds ratio	Parameter	Odds ratio
Migration year				
2007 versus 2008	−1.8 (−2.1, −1.4)	0.2 (0.1, 0.2)*		
2009 versus 2008	−1.3 (−1.5, −1.1)	0.3 (0.2, 0.3)*	−1.1 (−1.3, −0.8)	0.3 (0.3, 0.5)*
2010 versus 2008			−1.0 (−1.2, −0.7)	0.4 (0.3, 0.5)*
Out-migration timing				
Peak versus early	−0.2 (−0.5, 0.0)	0.8 (0.6, 1.0)*	−0.8 (−1.0, −0.5)	0.5 (0.4, 0.6)*
Late versus early	−1.0 (−1.2, −0.7)	0.4 (0.3, 0.5)*	−2.8 (−3.7, −1.9)	0.1 (0.0, 0.2)*
Fork length				
Fork length (1-cm increase)	0.2 (0.1, 0.2)	1.2 (1.1, 1.2)*	0.1 (0.1, 0.2)	1.1 (1.1, 1.2)*
Rearing type				
Wild versus hatchery	0.7 (0.5, 1.0)	2.1 (1.6, 2.8)*	0.2 (0.0, 0.5)	1.3 (1.0, 1.7)
Body injuries				
Absent versus severe	1.0 (0.4, 1.5)	2.6 (1.5, 4.4)*	0.7 (−0.2, 1.5)	1.9 (0.8, 4.5)
Moderate versus severe	0.5 (−0.2, 1.1)	1.6 (0.9, 2.9)*	0.6 (−0.3, 1.5)	1.8 (0.7, 4.4)
Absent versus moderate	0.5 (0.1, 0.9)	1.6 (1.2, 2.3)*	0.1 (−0.3, 0.4)	1.1 (0.8, 1.5)
Disease symptoms				
Absent versus severe	1.3 (−0.1, 2.7)	3.7 (0.9, 14.9)	1.5 (−0.5, 3.5)	4.5 (0.6, 33.1)
Moderate versus severe	0.8 (−1.0, 2.6)	2.2 (0.4, 13.1)	ND[a]	ND[a]
Absent versus moderate	0.5 (−0.6, 1.7)	1.7 (0.5, 5.4)	ND[a]	ND[a]
Fin damage				
Absent versus severe	0.2 (−0.1, 0.5)	1.2 (0.9, 1.7)	2.0 (0.1, 4.0)	7.7 (1.1, 55.2)*
Moderate versus severe	0.2 (0.0, 0.5)	1.3 (1.0, 1.6)	2.0 (0.1, 4.0)	7.7 (1.1, 55.3)*
Absent versus moderate	0.0 (−0.3, 0.2)	0.9 (0.7, 1.2)	0.0 (−0.2, 0.2)	1.0 (0.8, 1.3)

[a] ND = no data available; could not be estimated as no upper Columbia River steelhead with moderate disease symptoms returned as adults.

and 4.5 times (95% CI, 0.6–33.1), respectively, more likely to survive to adulthood than were steelhead with severe external disease symptoms (Table 4). Similarly, SR steelhead and UCR steelhead without body injuries were 2.6 times (95% CI, 1.5–4.4) and 1.9 times (95% CI, 0.8–4.5), respectively, more likely to survive to adulthood than were steelhead with severe body injuries (Table 4). The effect of fin damage on survival was much stronger for UCR steelhead (7.7 times more likely to survive) than for SR steelhead (1.2 times more likely to survive; Table 4). The greater effect of fin damage on survival of UCR steelhead was also demonstrated by inclusion of the fin damage variable in all the best-fit survival models for UCR steelhead (Table 3). Overall, qualitative results across both steelhead populations consistently indicated that steelhead without body injuries, disease symptoms, or fin damage were more likely to survive than were steelhead ranked as severe in any of these condition categories.

Decreases in survival were often commensurate with changes in the severity of external condition variables (Table 4). For instance, SR steelhead survival was highest for steelhead without body injuries, intermediate for steelhead with moderate body injuries, and lowest for steelhead with severe body injuries. Upper Columbia River steelhead survival was similar for fish with no or moderate body injuries, but lower for steelhead with severe body injuries (Table 4). In each steelhead DPS, fin damage was not associated with decreased survival until it became severe (Table 4). Conversely, the mere presence of external disease symptoms (moderate or severe) was associated with reduced survival relative to steelhead without disease symptoms. Specific parameter estimates comparing UCR steelhead with moderate disease symptoms could not be estimated because no juvenile UCR steelhead in this category of disease symptoms returned as an adult. Indirectly, the lack of any UCR steelhead with moderate disease symptoms that returned as adults corroborates the results from SR steelhead, where survival of SR steelhead was lower for juveniles with moderate disease symptoms than for those without disease symptoms (Table 4).

In addition to variables for external condition, the variable for FL of juvenile steelhead was always included in best-fit survival models for each steelhead DPS (Table 3). Results indicated that survival of juvenile steelhead to adulthood was positively correlated to juvenile FL. Correlations between juvenile FL and

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survival to adulthood were also quantitatively similar for each steelhead DPS, where survival odds for SR steelhead and UCR steelhead increased 1.2 times (95% CI, 1.1–1.2) and 1.1 times (95% CI, 1.1–1.2), respectively, for every 1-cm increase in juvenile FL (Table 4). The explanatory variable for rearing type also had strong support, as it was included in all best-fit survival models for SR steelhead and the top model for UCR steelhead (Table 3). Juveniles from SR and UCR classified as wild were associated with an increase in survival odds of 2.1 times (95% CI, 1.6–2.8) and 1.3 times (95% CI, 1.0–1.7), respectively, relative to juveniles classified as hatchery origin (Table 4).

Inclusion of population-level variables (year and timing) was also strongly supported in the top models for both SR steelhead and UCR steelhead. Models that included variables for year and timing had much more support relative to null models (Table 3). Results from this study indicated that juvenile-to-adult survival in both UCR steelhead and SR steelhead was highest for juveniles that out-migrated in 2008 (Table 4; Figure 2). Survival odds for juveniles that out-migrated during the early period were higher than for those that out-migrated during peak and late periods. Again, the finding of higher survival for early migrants was consistent across both the UCR steelhead and SR steelhead DPSs (Table 4; Figure 2).

Model-averaged individual steelhead survival rates generally ranged from <0.1% to >20.0% depending on when a steelhead migrated (year and timing) and the individual characteristics of that steelhead (length, rearing type, and external condition; Figure 2). Fitted survival rates for SR steelhead had similar trends as those for UCR steelhead (Figure 2). Variation in the condition, length, and rearing type of juvenile steelhead (Table 1) led to substantial variation in survival rates within each population-level category (Figure 2). Survival rates for juveniles that out-migrated during the early period were generally higher than those that out-migrated during the peak or late periods (Table 4). Variation within these periods, however, was often substantial once individual fish characteristics were accounted for (Figure 2). For instance, the predicted median for juvenile-to-adult survival rates for SR steelhead that out-migrated during the peak period of 2008 was 5.0%; however, due to variation in individual fish characteristics, survival rates across individuals varied from 1.3% to 10.2% during that period (Figure 2a).

DISCUSSION

Results of this study indicated that individual fish characteristics recorded during the juvenile life stage were important factors in predicting the probability of steelhead surviving to adulthood. Qualitative and quantitative similarities in population-level and individual-level results for both the SR steelhead and UCR steelhead DPSs suggest these two populations experience similar mortality factors during out-migration and ocean residency. This is not surprising given that the SR steelhead and UCR steelhead used in this study shared the same migration corridor (Columbia River) following tagging and release. Little is known, however, about salmonid mortality factors in the ocean and whether differences in mortality rates exist within and among salmonid populations following out-migration (Petrosky and Schaller 2010). Similar to Haeseker et al. (2012), our results support the hypothesis that similar factors may influence freshwater and marine survival across salmonid populations either due to co-existence during these life stages or to roughly equivalent mortality factors that affect each population.

External maladies identified in this study have been linked to multiple health and survival performance metrics in salmonids. The most consistent external condition variables associated with survival to adulthood were measures of tissue damage (body injuries, fin damage) and disease (bacterial, fungal, or viral infections). These maladies have been linked to decreased swimming performance (Hansen 1988), increased susceptibility to predation (Mesa et al. 1994, 1998; Hostetter et al. 2012), internal fish condition (Hostetter et al. 2011), and reduced juvenile survival (Nicola and Cordone 1973; Arkoosh et al. 2006; Hostetter et al. 2011). Rapid, nondestructive examination procedures only provide proxy measures of fish health (Hostetter et al. 2011). Nondestructive techniques can be particularly useful, however, when external measures are correlated with internal measures of fish health (Hostetter et al. 2011; Connon et al. 2012) and when the fish characteristics are proven performance metrics of survival. Results of this study validated the rapid, nondestructive examination techniques developed in Hostetter et al. (2011) as performance metrics associated with juvenile-to-adult survival across steelhead DPSs.

Numerous other studies support a positive correlation between juvenile salmonid length and survival, both for juvenile survival (Zabel and Achord 2004; Zabel et al. 2005) and juvenile-to-adult survival (Ward and Slaney 1988). Length-related survival advantages may be associated with longer steelhead being less susceptible to predation (Mesa et al. 1994; Hostetter et al. 2012) and/or having other competitive advantages related to increased swimming performance and energy reserves (Zabel and Achord 2004). Results from this study also indicated that after accounting for differences in fish length, external condition, and out-migration timing, hatchery fish were less likely to survive to adulthood than were wild fish, especially in SR steelhead. Previous research supports this finding. Newman (1997) found that hatchery juvenile steelhead from the Columbia River basin were significantly less likely to survive out-migration than were wild fish, and Haeseker et al. (2012) found that the annual percentage of SR hatchery steelhead in the population was negatively related to adult return rates.

The most parsimonious models predicting juvenile-to-adult survival for SR steelhead and UCR steelhead included both individual-level variables and population-level variables (year and out-migration timing). Differences in return rates by year have been attributed to differences in river conditions (temperature, flow), hydroelectric dam operational strategies (spill, juvenile fish transportation), and ocean conditions (Sandford

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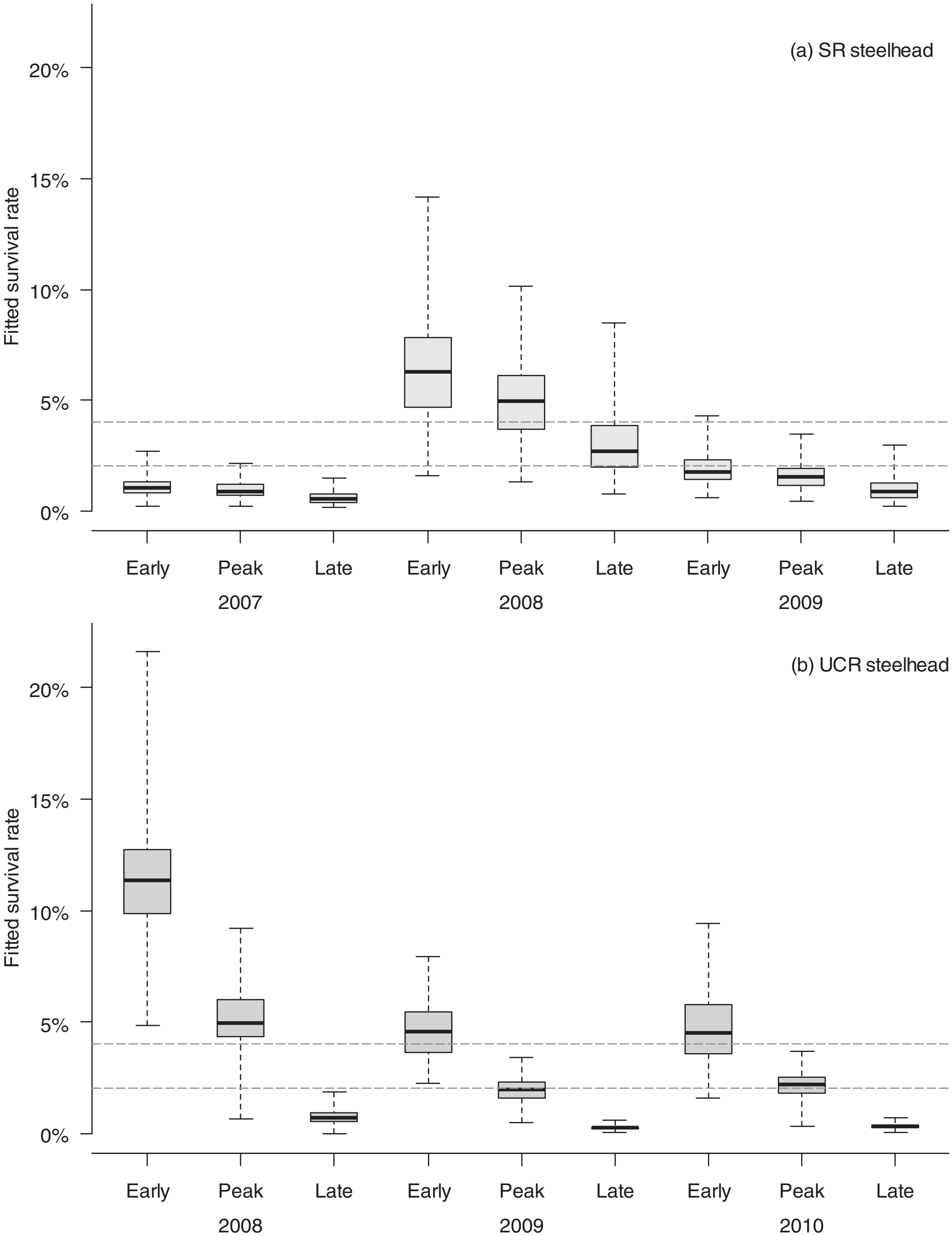

FIGURE 2. Model-averaged juvenile-to-adult survival rates for individual (**a**) Snake River (SR) steelhead and (**b**) upper Columbia River (UCR) steelhead as a function of out-migration timing. Juvenile out-migration years were 2007–2009 for SR steelhead (n = 25,959) and 2008–2010 for UCR steelhead (n = 21,739). Vertical error bars encompass 95% of the fitted individual survival rates. Horizontal dashed lines represent the minimum (2%) and average (4%) juvenile-to-adult survival management goals (NPCC 2009).

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and Smith 2002; Scheuerell at al. 2009; Haeseker et al. 2012). In addition to annual differences in survival, results presented here also indicated that early migrating SR and UCR steelhead were significantly more likely to return as adults than were juveniles that migrated during the peak or late out-migration periods. Sandford and Smith (2002) hypothesized that early migrating juveniles may experience optimal ocean foraging conditions and reduced predation during out-migration. Petrosky and Schaller (2010) found that juvenile-to-adult survival was associated with water velocities, whereby return rates were highest for groups of fish migrating during high flow events, which often occurs during the early and peak out-migration periods. Haeseker et al. (2012) found that adult survival rates were associated with water transit times, spill patterns, and ocean conditions experienced by juvenile SR steelhead, all of which vary by year and out-migration timing. In addition to these environmental factors, results of this study clearly indicated that the individual-level variables of fish condition, size, and rearing-type also play an integral role in survivorship to adulthood and, as such, studies that include both population- and individual-level variables will provide the most comprehensive evaluation of the mechanisms that influence survival.

Data on fish condition will only be useful to fisheries managers if the condition variables are associated with differences in survival and are present and measurable in the population at large. For both UCR and SR steelhead, individual-level variables were both associated with survival and present in the population. For instance, 3, 7, and 22% of SR steelhead had severe external symptoms of disease, body injuries, or fin damage, respectively. Although the presence of some external conditions was sometimes low (<5%), the combination of numerous individual fish characteristics associated with survival and variation in those factors led to substantial variation in fitted survival probabilities across individuals. Capturing this variation may not only lead to a better understanding of the factors that influence survival but it may result in more accurate estimates of fish survival at the population level. Conversely, ignoring naturally occurring variation in individuals from a population, for example, by culling fish for tagging studies based on their external condition, length, or rearing type, will influence survival estimates for the population to varying degrees. Furthermore, quantifying changes in individual fish characteristics that take place during out-migration, which were not captured in the present study, and relating those changes to fish survival remains an important but unaddressed goal.

Despite the importance of individual-level variables in describing survivorship to adulthood, results of this study indicated that managing for optimal fish characteristics (condition, size, and rearing type) may not by itself increase steelhead survival above target juvenile-to-adult thresholds in all years. In years when survival was very poor (e.g., 2007), juvenile-to-adult survival was below the minimum 2% goal for nearly all steelhead sampled, regardless of fish condition, size, rearing type, and out-migration timing. In years when survival was higher, however, variation in return rates was much greater, and opportunities to further increase survival above stated survival goals through management may exist. For example, management efforts to increase flows to reduce water transit times so fish reach the ocean more quickly could increase survival (Scheuerell et al. 2009; Haeseker et al. 2012). Efforts to reduce fish injury rates by modifying dam and dam operational strategies (Johnson et al. 2000; Muir et al. 2001; Ferguson et al. 2007), along with efforts to reduce disease and disease transmission (Loge et al. 2005; Arkoosh et al. 2006) may also increase adult returns. Finally, increasing the size and overall health of out-migrating juveniles may bolster adult return rates of steelhead and perhaps other anadromous salmonids.

Monitoring of demographic data are often incorporated in recovery plans for fish listed under the ESA (Campbell et al. 2002), including numerous ESA-listed Columbia River basin salmonid populations (FPC 2012). Results from this study showed that collection and application of individual-level fish characteristics, including fish condition, provided an important understanding of factors associated with juvenile-to-adult survival rates in two distinct steelhead populations. The proximate causes of fish damage and degradation, however, remain unknown. Furthermore, whether individual measures of fish condition change during out-migration and whether the trends observed for steelhead in this study apply to other anadromous species remain unknown and should be the focus of future studies involving individual fish characteristics and survival.

ACKNOWLEDGMENTS

We thank B. Cramer, J. Tennyson, M. Carper, P. Loschl, and numerous technicians for their help in the field. The U.S. Army Corps of Engineers, Walla Walla District, provided funding to tag juvenile fish used in this study, for which we are grateful. We especially thank M. Plummer, B. Spurgeon, D. Tratchenbarg, and C. Pinney for providing access to Snake River dams and for providing logistical support. We thank the Chelan County Public Utility District, particularly S. Hemstrom and B. Keesee, for providing access to Rock Island Dam and for allowing us to work with their staff at the juvenile fish facility. The use of trade or product names does not constitute endorsement by the U.S. Government. All handling of live fish as part of this study followed protocols approved by the Institutional Animal Care and Use Committee at Oregon State University.

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APPENDIX: MODEL PERFORMANCE DATA

Table A.1 . Relative performance of models predicting survival of juveniles to adulthood for Snake River steelhead and upper Columbia River steelhead. Variables are year (Y), out-migration timing (T), fork length (L), rearing-type (REAR), body injuries (BODY), descaling (DESCALE), external symptoms of disease (DISEASE), ectoparasites (PARA), and fin damage (FIN); see Table 1 for variable descriptions. K is the number of parameters, $\Delta \mathrm{AIC}_c$ is the difference in AIC_c between the top-ranked model and the model of interest, and AIC_c weights (AIC_c w) indicate relative support for any particular model. All models with AIC_c $w > 0.01$, the best model without individual fish characteristics (Y + T), and the null model are shown.

Model	K	AIC_c	$\Delta\mathrm{AIC}_c$	AIC_c w
Snake River steelhead				
Y + T + L + REAR + DISEASE + BODY	11	4,161.58	0.00	0.30
Y + T + L + REAR + DISEASE + BODY + FIN	13	4,161.92	0.34	0.25
Y + T + L + REAR + BODY + FIN	11	4,163.99	2.42	0.09
Y + T + L + REAR + BODY	9	4,164.03	2.45	0.09
Y + T + L + REAR + DISEASE + DESCALE + BODY	13	4,164.95	3.38	0.06
Y + T + L + REAR + DISEASE + DESCALE + BODY + FIN	15	4,165.24	3.66	0.05
Y + T + L + REAR + DISEASE + BODY + PARA	13	4,165.38	3.81	0.04
Y + T + L + REAR + DISEASE + BODY + FIN + PARA	15	4,165.72	4.14	0.04
Y + T + L + REAR + DESCALE + BODY + FIN	13	4,167.27	5.70	0.02
Y + T + L + REAR + DESCALE + BODY	11	4,167.36	5.78	0.02
Y + T + L + REAR + BODY + FIN + PARA	13	4,167.79	6.22	0.01
Y + T + L + REAR + BODY + PARA	11	4,167.83	6.26	0.01
Y + T + L + REAR + DISEASE + DESCALE + BODY + PARA	15	4,168.76	7.18	0.01
Y + T + L + REAR + DISEASE + DESCALE + BODY + FIN + PARA	17	4,169.04	7.46	0.01
Y + T	5	4,261.84	100.26	0.00
Null	1	4,487.04	325.46	0.00
Upper Columbia River steelhead				
Y + T + L + DISEASE + FIN + REAR	11	3,640.88	0.00	0.24
Y + T + L + DISEASE + FIN	10	3,642.23	1.35	0.12
Y + T + L + DISEASE + FIN + REAR + BODY	13	3,642.30	1.43	0.12
Y + T + L + DISEASE + FIN + REAR + PARA	13	3,643.66	2.78	0.06
Y + T + L + DISEASE + FIN + BODY	12	3,643.69	2.81	0.06
Y + T + L + DISEASE + FIN + PARA	12	3,644.06	3.18	0.05
Y + T + L + DISEASE + FIN + REAR + DESCALE	13	3,644.57	3.69	0.04
Y + T + L + FIN + REAR + BODY	11	3,645.06	4.18	0.03
Y + T + L + DISEASE + FIN + REAR + BODY + PARA	15	3,645.08	4.20	0.03
Y + T + L + DISEASE + FIN + BODY + PARA	14	3,645.51	4.63	0.02
Y + T + L + DISEASE + FIN + DESCALE	12	3,645.79	4.91	0.02
Y + T + L + DISEASE + REAR	9	3,645.84	4.96	0.02
Y + T + L + DISEASE + FIN + REAR + BODY + DESCALE	15	3,646.11	5.23	0.02
Y + T + L + FIN + REAR	9	3,646.21	5.33	0.02
Y + T + L + FIN + BODY	10	3,646.56	5.68	0.01
Y + T + L + DISEASE + REAR + BODY	11	3,646.76	5.88	0.01
Y + T + L + DISEASE + FIN + REAR + PARA + DESCALE	15	3,647.34	6.46	0.01
Y + T + L + DISEASE + FIN + BODY + DESCALE	14	3,647.39	6.51	0.01
Y + T + L + DISEASE + FIN + PARA + DESCALE	14	3,647.63	6.75	0.01
Y + T + L + FIN	8	3,647.73	6.85	0.01
Y + T + L + DISEASE	8	3,647.81	6.93	0.01
Y + T + L + FIN + REAR + BODY + PARA	13	3,647.84	6.96	0.01
Y + T + L + FIN + BODY + PARA	12	3,648.37	7.49	0.01
Y + T	5	3,685.45	44.57	0.00
Null	1	3,871.03	230.15	0.00

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