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ARTICLE

Relationship of External Fish Condition to Pathogen Prevalence and Out-Migration Survival in Juvenile Steelhead

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Abstract

Understanding how the external condition of juvenile salmonids is associated with internal measures of health and subsequent out-migration survival can be valuable for population monitoring programs. This study investigated the use of a rapid, nonlethal, external examination to assess the condition of run-of-the-river juvenile steelhead *Oncorhynchus mykiss* migrating from the Snake River to the Pacific Ocean. We compared the external condition (e.g., body injuries, descaling, external signs of disease, fin damage, and ectoparasite infestations) with (1) the internal condition of a steelhead as measured by the presence of selected pathogens detected by histopathology and polymerase chain reaction analysis and (2) out-migration survival through the Snake and Columbia rivers as determined by passive integrated transponder (PIT) tag technology. The results from steelhead captured and euthanized ($n = 222$) at Lower Monumental Dam on the lower Snake River in 2008 indicated that external condition was significantly correlated with selected measures of internal condition. The odds of testing positive for a pathogen were 39.2, 24.3, and 5.6 times greater for steelhead with severe or moderate external signs of disease or more than 20% descaling, respectively. Capture–recapture models of 22,451 PIT-tagged steelhead released at Lower Monumental Dam in 2007–2009 indicated that external condition was significantly correlated with juvenile survival. The odds of out-migration survival for steelhead with moderate or severe external signs of disease, more than 20% descaling, or

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severe fin damage were 5.7, 4.9, 1.6, and 1.3 times lower, respectively, than those for steelhead without these external conditions. This study effectively demonstrated that specific measures of external condition were associated with both the internal condition and out-migration survival of juvenile steelhead.

In their natural environments, fish are subjected to numerous stressors that impair their physical condition (Wedemeyer et al. 1984; Adams 1990). Poor physical condition can reduce fish survival directly by altering aspects of performance, such as immune suppression (Peters et al. 1988; Arkoosh 2006), providing entry sites for pathogens (Goede and Barton 1990), adversely affecting a fish's ability to avoid predation (Olla et al. 1992; Mesa 1994; Mesa et al. 1994), or decreasing a fish's ability to cope with other environmental challenges (Schreck 1990; Pickering 1993; Wendelaar Bonga 1997). There is general agreement that fish condition affects survival (Barton et al. 2002; Budy et al. 2002), but there is surprisingly little published quantitative data on how external fish conditions are associated with subsequent in-river survival (e.g., Keefer et al. 2008).

Numerous techniques have been used to evaluate fish condition, and they can be broadly categorized as clinical (i.e., physiological, biochemical, or histopathological; Neff 1985; Adams 1990; Niimi 1990) or observational (i.e., based on external appearance and organosomatic indices; Goede and Barton 1990; Adams et al. 1993). Many of these techniques require lethal sampling of a representative proportion of the population of interest. Lethal collection of fish may not be appropriate nor the best alternative for studies involving (1) small populations, (2) species listed as threatened or endangered, (3) logistical or funding constraints, or (4) if study objectives address linkages between fish condition and behavior, movement, or postrelease survival.

Declines of populations of Pacific salmonids *Oncorhynchus* spp. in the Columbia River basin led the National Marine Fisheries Service (NMFS) to list 13 of 20 evolutionarily significant units (ESUs) of salmonids as threatened or endangered under the U.S. Endangered Species Act (ESA; Waples 1991; Good et al. 2005), including the Snake River steelhead *O. mykiss* ESU. The listing status of Columbia River basin salmonids has lead to the implementation of extensive nonlethal monitoring programs that capture and externally examine thousands of juvenile salmonids emigrating from the Columbia and Snake river basins to assess their population status and factors affecting survival (FPC 2010). During their out-migration, juvenile salmonids must pass up to eight main-stem hydroelectric dams, most of which have juvenile by-pass facilities where these fish can be collected and interrogated for this purpose. Although Snake River steelhead have been the subject of extensive research, monitoring, and evaluation since the development of the Columbia and Snake river hydrosystem (Budy et al. 2002; Schreck et al. 2006), little is known regarding how fish condition and health relates to the subsequent in-river smolt survival.

The main objective of this study was to investigate whether the external condition of juvenile steelhead as measured by a rapid, nondestructive examination procedure can be used as an index of the fish's internal condition and a predictor of its subsequent out-migration survival probability. We evaluated how steelhead external condition (e.g., body injuries, descaling, external signs of disease, fin damage, and ectoparasite infestations) was associated with (1) the internal condition as measured by the presence of selected pathogens detected by histopathology and polymerase chain reaction (PCR) analyses, and (2) out-migration survival through the Snake and Columbia rivers (approximately 354 river kilometers [rkm]) as measured by interrogation of fish tagged with passive integrated transponders (PIT) at in-river locations downstream from release sites. The management implications of our study results and the feasibility of incorporating these observational techniques to assess fish condition as part of a comprehensive fish population monitoring program are also discussed.

METHODS

Fish capture and tagging.—Run-of-the-river juvenile steelhead out-migrating from the Snake River basin were collected at the LMN Dam juvenile fish collection facility (rkm 589; Figure 1). In general, steelhead were collected at least 5 d per week throughout the juvenile steelhead out-migration, from early April to early July, in 2007, 2008, and 2009. Before our sampling, fish captured at LMN Dam were held in a 7,500-L holding tank with flow-through river water for up to 24 h. Daily samples of captured juvenile steelhead were separated into small batches (10–50 fish) via a slide gate, anesthetized with tricaine methanesulfonate (MS-222), and tagged with a passive integrated transponder (PIT) tag via a modified hypodermic syringe with a 12-gauge needle (Prentice et al. 1990a, 1990c; Nielson 1992). To reduce pathogen transmission, needles were soaked for a minimum of 10 min in 70% ethyl alcohol before PIT tag loading.

External condition.—After a steelhead was PIT-tagged, it was placed in a sample tray, measured (fork length [FL], nearest millimeter), weighed (nearest gram), assigned as originating from a hatchery or wild rearing environment (presence of a clipped adipose fin or erosion of pectoral, pelvic, caudal, or dorsal fins), scored for overall external condition (good, fair, poor; modified version of the procedure developed by Evans et al. 2004), and digitally photographed (Canon EOS Rebel XTi camera; Canon EF 50 mm lens f/2.5 Compact Macro lens; Bencher Copymate II copy stand with fluorescent producer light source).

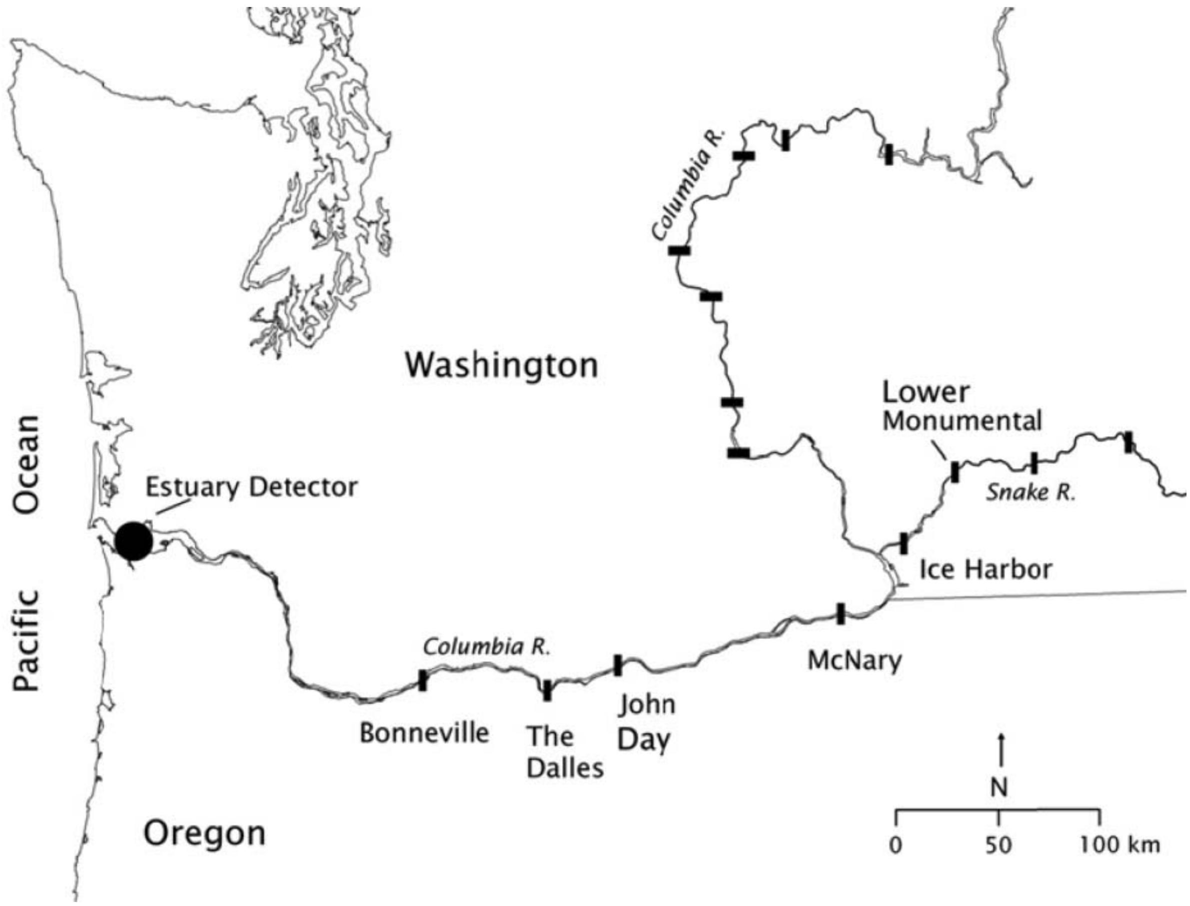

FIGURE 1. Map of the main-stem Snake and Columbia rivers with major hydroelectric dams denoted by bars. Juvenile steelhead PIT-tagged and released from Lower Monumental Dam were potentially detectable as they passed Ice Harbor, McNary, John Day, and Bonneville dams as well as a net-mounted detector deployed from a pair trawl in the estuary.

Digital photographs were taken of both sides of the steelhead to allow for detailed classification of external conditions by type and severity after the study fish was released thereby reducing the total handling time for each fish (<30 s). Detailed information on the external condition (e.g., body injuries, descaling, external signs of disease, fin damage, and ectoparasite infestations; Table 1) of each study fish was collected by analyzing digital photographs, and the information was stored in the same database containing the photos and tagging information.

Internal condition.—To investigate the associations between external and internal fish condition, we euthanized a subsample of juvenile steelhead that were collected at LMN Dam in 2008. At least 60 individuals in each integrated condition rank (i.e., good, fair, poor; Table 1) were euthanized for later laboratory analyses. Internal condition was assessed based on histopathology measures and polymerase chain reaction analyses.

Histopathology measures were used to determine the presence of infection following diagnostic procedures (Erickson and Wallace 1959; Noga 1996). Once euthanized, sections of a steelhead's gills and internal viscera (kidney, liver, spleen, heart, and gastrointestinal tract) were placed into a tissue cassette for histopathology analyses. Tissue cassettes were uniquely labeled for each steelhead and then immersed for 72 h in 10% neutral-buffered formalin with a final minimum volume of 1 part tissue to 10 parts formalin (Hopwood 1990; Bancroft and Stevens 1994; Presnell and Schreibman 1997). After routine processing, the formalin-fixed tissue samples were embedded in paraffin and sectioned at a thickness of 5 μm. Slides containing tissue sections were subsequently stained with hematoxylin and eosin (Bancroft and Stevens 1994; Presnell and Schreibman 1997). Specifically, for each fish, two sections of each organ or tissue were microscopically examined to determine presence of infection by means of diagnostic procedures and keys used to identify specific organisms of interest (Erickson and Wallace 1959; Noga 1996; Hoffman 1999).

Nine salmonid pathogens (Table 2), including viral, algal (fungal-like), and bacterial microorganisms, were surveyed in anterior head kidney tissue by the detection of their genetic material with PCR analyses (unless otherwise noted, all materials used in PCR analyses were provided by Applied Biosystems,

TABLE 1. Description and prevalence of external measures of condition in steelhead captured at Lower Monumental Dam in 2007, 2008, and 2009. Captured steelhead were either tagged with a passive integrated transponder (PIT) tag and released ($n = 22{,}451$) or euthanized for evaluation of internal condition ($n = 222$).

External condition	Prevalence[a]	Number PIT-tagged	Number euthanized[b]	Description
Body injury				
Absent	81%	18,151	116	No visible hemorrhaging, scarring, or other damage to the head, trunk, operculum, or eyes
Moderate	12%	2,609	39	Closed or healed scars to the head, trunk, operculum, or eyes
Severe	8%	1,691	67	Deformities, open wounds, or large surface area scarring on the head, trunk, operculum, or eyes
Descaling				
<5%	66%	14,834	80	Loss of scales on less than 5% of body
5–20%	30%	6,791	93	Loss of scales on 5–20% of body
>20%	4%	826	49	Loss of scales on more than 20% of body
Diseased				
Absent	96%	21,601	164	No external signs of bacterial, fungal, or viral infections
Moderate	1%	323	6	Visible infection limited to one external area
Severe	2%	527	52	Visible infection in multiple areas or signs that suggest a systemic infection
Ectoparasites				
Absent	97%	21,828	211	No visible ectoparasites
Moderate	2%	466	5	Visible ectoparasites in one area
Severe	1%	157	6	Visible ectoparasites in more than one area or on gills
Fin damage				
Absent/minor	23%	5,138	43	Fin wear and damage less than 50% on any fin
Moderate	56%	12,578	108	Fin wear and damage greater than 50% on one or two fins
Severe	21%	4,735	71	Fin wear and damage greater than 50% on three or more fins
Integrated condition[c]				
Good	59%	13,185	61	No noticeable external injury or signs of disease; descaling no more than 10% of body surface
Fair	28%	6,218	62	Minor scars or other closed external damage; descaling greater than 10% but no more than 50% of body surface
Poor	14%	3,048	99	External signs of fungal, parasitic, or bacterial infections, descaling greater than 50% of body surface, or open external body lesions

[a]Percentage of PIT-tagged steelhead that exhibited each external condition measure.
[b]Steelhead were euthanized in 2008 only.
[c]Modified version of the procedure developed by Evans et al. (2004) for scoring external condition in adult steelhead.

Foster City, California). A small (~25-mg) piece of anterior head kidney was aseptically collected from each euthanized steelhead. Kidney samples were placed in iced 96-well plates containing RNAlater preservative (Qiagen, Valencia, California) and stored at −20°C within 3 h of collection and until nucleic acid extraction. Both DNA and RNA were extracted from kidney tissue by means of DNeasy 96 Blood and Tissue kit and RNeasy 96 kit, respectively (Qiagen, Valencia, California). Purified RNA was immediately converted to complementary DNA (cDNA) with the High Capacity cDNA Archive Kit. Both DNA and cDNA were diluted 1:10 with RNase-free water. Purified nucleic acids were stored at −20°C before PCR analyses. The PCR was performed on a 10-μL volume containing: 1.5–5 mM $MgCl_2$, 10× Buffer II, 800 nM of each primer, 800 μM deoxynucleotide triphosphate (dNTP), 0.5 U of AmpliTaq Gold DNA polymerase, and 3 μL DNA or cDNA (nondilute and 1:10). Primers were labeled with either FAM, VIC, or NED fluorescent dyes for subsequent detection by capillary electrophoresis.

TABLE 2. Methods used in polymerase chain reaction analyses of nine salmonid pathogens in steelhead anterior head kidney tissue.

Pathogen	Reference
Aeromonas hydrophila	Dorsch et al. (1994)
Listonella anguillarum	Hong et al. (2007)
Flavobacterium columnare	Welker et al. (2005)
Yersinia ruckeri	Del Cerro et al. (2002)
Renibacterium salmoninarum	Modified from Chase and Pascho (1998)
Aeromonas salmonicida	Del Cerro et al. (2002)
Infectious hematopoietic necrosis virus	Williams et al. (1999)
Viral hemorrhagic septicemia virus	Williams et al. (1999)
Saprolegniaceae family	Dieguez-Uribeondo et al. (2007)

Amplification was performed with a GeneAmp 9700 thermalcycler according to the referenced literature (Table 2). Amplified DNA was stored at 4°C before fragment analyses. All fragment analyses were performed on an Applied Biosystems DNA analyzer 3730xl. Up to four PCR products were added to a sequencing cocktail consisting of GeneScan LIZ1200 size standard and Hi-Di Formamide and denatured for 5 min before fragment analysis. Raw data output from the DNA analyzer was imported into GeneMapper (version 3.7) software and analyzed for the presence of size-specific peaks, which represent positive PCR products of targeted pathogens. Peaks within 2 base pairs (bp) of the anticipated PCR product size and at least twice the intensity of the background noise were scored as positive.

Relationship between internal and external fish condition.—The internal condition of each fish was scored as a single binary measure representing either (0) the absence of all pathogens (assessed by PCR) and infections (assessed by histopathology) or (1) the presence of one or more pathogens or infections. Only two pathogens were identified by PCR: *Renibacterium salmoninarum* (the causative agent of bacterial kidney disease), and infectious hematopoietic necrosis virus (IHNV). Additionally, infection presence, as identified by histopathology analyses, was associated with only three types of organisms: mycotic (fungal), parasitic trematodes (*Sanguinicola* spp.), and gill amoebae. Hence, the binary measure of internal condition represented the absence or presence of one or more of these five organisms in fish tissue.

Logistic regression was used to evaluate how specific measures of external condition were associated with internal condition (Hosmer and Lemeshow 2000). We included variables for run stage (based on when the first 10% [early], middle 80% [peak], and last 10% [late] of the out-migrating juvenile steelhead population passed LMN Dam; FPC 2010) and rearing type (hatchery or wild) to control for these confounding variables in all regression models. The association between external condition measures and internal condition was then assessed by evaluating parameter estimates and odds ratios associated with each external condition measure after accounting for other external conditions, run timing, and rearing type. The odds of an event occurring are defined as the ratio of the probability that it will occur (P) to the probability that it will not occur ($1 - P$), that is,

$$\text{Odds} = \frac{P}{(1 - P)}.$$

A useful quantity to present results when comparing two groups in logistic regression is the odds ratio. In this study, odds ratios were used to express the relative odds of an event occurring when two levels of external condition measurements were compared (e.g., levels x or y), that is,

$$\text{Odds ratio}_x = \frac{P_x/(1 - P_x)}{P_y/(1 - P_y)}.$$

An odds ratio of 1.0 indicated that the probability of an event occurring was equal between two groups, whereas odds ratios greater than 1.0 indicated that the odds of occurrence were greater for group 1 compared with group 2. Logistic regression provided an equation for the natural logarithm of the odds of an event occurring. Back-transformed logistic regression coefficients were then used to present results in terms of odds ratios. Logistic regression models were evaluated for goodness of fit (Pearson's χ^2) and the covariance matrices were corrected if overdispersion was detected. Analyses were conducted with SAS, version 9.2 (SAS Institute, Inc., Cary, North Carolina), with statistical significance set at $\alpha = 0.05$.

Survival analysis.—The handling and external examination of steelhead chosen for survival analysis was identical to that of euthanized steelhead, except that steelhead captured for survival analysis were captured over a 3-year period (2007–2009), PIT-tagged, and released. Additionally, steelhead sampled for survival analysis were collected and PIT-tagged regardless of their condition, rearing type, or length in an effort to represent the overall population of steelhead collected at LMN Dam. After the examination process, PIT-tagged steelhead were placed in a 1,100-L holding tank with flow-through river water for 4–18 h, and then released into the LMN Dam tailrace via the juvenile bypass facility out-flow pipe. The number of fish released at a given time varied, but never exceeded 300 fish per release group. Release times alternated between 1800 hours and 2300 hours the same day as processing occurred and between 0600 hours and 1100 hours the day after processing to reduce possible bias in survival associated with release time. All mortalities and ejected PIT tags were removed from the temporary holding tank before release and excluded from further analysis.

Steelhead with PIT tags released into the tailrace of LMN Dam can be detected when passing downstream detection sites at Ice Harbor (ICH) Dam (rkm 538), McNary (MCN) Dam (rkm 470), John Day (JDA) Dam (rkm 347), Bonneville (BON) Dam (rkm 235), and finally, by a net-mounted detector deployed daily during the smolt out-migration period by pair-trawlers in the Columbia River estuary (EST, rkm 75; our Figure 1; Prentice et al. 1990b; Ledgerwood et al. 2004). Detection data from these locations were retrieved from the PIT Tag Information System (PTAGIS) maintained by the Pacific States Marine Fisheries Commission (PSMFC, Gladstone, Oregon). A detection history was constructed to record where each unique PIT tag code was or was not detected. Apparent survival probabilities for cohorts of steelhead, using both grouping variables (e.g., detection location, migration year, and run stage) and individual characteristics (e.g., fish length, fish origin, external conditions), were estimated with Cormack–Jolly–Seber (CJS) capture–recapture models (Cormack 1964; Jolly 1965; Seber 1965) implemented in Program MARK (White and Burnham 1999).

Previous studies have indicated that both environmental factors and individual characteristics can influence juvenile steelhead survival and detection probability at dams on the Columbia and Snake rivers (Skalski 1998; Muir et al. 2001; Zabel et al. 2005; Plumb et al. 2006). To best address our hypotheses regarding associations among external condition measures and survival, we included grouping variables for detection location, migration year, and run stage, along with individual covariates for FL and fish origin in both survival (φ) and detection probability (p) models.

We used a multistep approach to develop models that investigated the association between steelhead external condition and apparent survival. We separated our analyses to investigate survival at two different migration distances: short-distance survival (LMN Dam to MCN Dam, ~119 rkm) and long-distance survival (LMN Dam to BON Dam, the lowest dam on the Columbia River, ~354 rkm). Short-distance survival analysis incorporated all steelhead released from LMN Dam, and detection histories from MCN Dam and a pooled third occasion, which included all detection locations below MCN Dam (JDA Dam, BON Dam, and EST; Zabel et al. 2005). Long-distance survival analysis included all steelhead released from LMN Dam and detection histories from BON Dam and EST, which represented apparent survival through the hydrosystem from LMN Dam. Our overall modeling approach was to (1) evaluate goodness of fit and estimate an overdispersion parameter ($\hat{c}$) for our most general model of grouping variables [(φ location $\times$ run stage $\times$ year) p(location $\times$ run stage $\times$ year)] using the bootstrap procedure in Program MARK, (2) correct the covariance matrices for this overdispersion ($\hat{c} = 1.383$; 95% confidence interval [CI], 1.362–1.404; 500 simulations), (3) model both short-distance and long-distance migration survival with an additive survival model that included variables for detection location, migration year, run stage, FL, rearing type, and external condition measures and an additive detection probability model that included variables for detection location, migration year, run stage, FL, and rearing type, and (4) assess the association between external condition measures and apparent survival by evaluating the parameter estimates and odds ratios of each external condition measure. Survival estimates and 95% CIs that incorporate variance associated with all factors contributing to survival probabilities are also presented. Overall, this modeling structure allowed us to identify associations between specific external conditions and apparent survival over two migration distances, after accounting for other external conditions and additional expected sources of variation in steelhead detection and survival probabilities.

RESULTS

Fish Capture, Tagging, and In-River Interrogation

A total of 22,451 (19,089 hatchery-reared and 3,362 wild) steelhead were PIT-tagged and released at LMN Dam as part of this study. Numbers of PIT-tagged steelhead released from LMN Dam varied among 2007 ($n = 6{,}247$), 2008 ($n = 7{,}919$), and 2009 ($n = 8{,}285$), but comprised about 1% of all steelhead passing LMN Dam in each year. Similarly, the proportion of hatchery-reared (85%) and wild (15%) steelhead PIT-tagged and released as part of this study corresponded with the overall proportion of hatchery and wild steelhead collected at LMN Dam. Downstream detections of the 22,451 PIT-tagged steelhead released from LMN Dam included 3,054 steelhead detected at MCN Dam (14%), 2,736 steelhead detected at JDA Dam (12%), 2,081 steelhead detected at BON Dam (9%), and 304 steelhead detected at EST (1%).

External Condition

Fin damage was the most prevalent external condition (77% of all steelhead sampled), followed by more than 5% descaling (34%), body injuries (20%), external signs of disease (3%), and ectoparasites (3%; Table 1). Numerous steelhead displayed multiple external conditions (see Table A.2 in the appendix). The prevalence of external conditions varied by run stage, and steelhead captured during the late run had a higher prevalence of moderate body injuries (5% higher), severe body injuries (5% higher), and more than 20% descaling (3% higher) compared with steelhead that migrated earlier in the season. However, both moderate signs of disease (2% higher) and severe signs of disease (2% higher) were more prevalent during the early run stage.

Internal Condition

Juvenile steelhead lethally collected for analysis of internal condition were captured between 24 April and 22 June 2008. Of the 222 steelhead collected, 106 (48%) tested positive for an internal condition (presence of mycotic organisms, trematodes [*Sanguinicola* spp.], gill amoebae, *R. salmoninarum*, or IHNV). Of the 106 steelhead that tested positive for an internal condition, 82 (77%) tested positive for only one infection, 24 (23%) tested positive for two infections, and no fish tested positive for more than two infections. Overall, mycotic infections were the most prevalent internal condition (27%), followed by trematode infection (16%), presence of *R. salmoninarum* (8%) in kidney tissue, presence of IHNV (5%) in kidney tissue, and gill amoeba infection (3%). Of the 106 steelhead that tested positive for an internal condition, 54 (51%) had moderate or severe external signs of disease.

After accounting for rearing type and run stage, internal condition was associated with steelhead external condition. Using our a priori integrated condition ranks, the odds of having an internal condition for steelhead in poor condition were 5.6 times (95% CI: 1.8–17.9, $P = 0.004$) and 6.2 times (95% CI: 2.0–20.0, $P = 0.002$) greater than those for steelhead in good or fair condition, respectively. There was no evidence, however, that steelhead in fair condition were more likely to have an internal condition compared with steelhead in good condition ($P = 0.866$) (Table 3).

Specific external conditions associated with the internal condition of a steelhead included external signs of disease and descaling (Table 3). Steelhead with moderate or severe external signs of disease had odds of an internal condition that were 24.3 times (95% CI: 2.5–240.9, $P = 0.006$) and 39.2 times (95% CI: 10.0–153.3, $P < 0.001$) greater than steelhead without external signs of disease, respectively. No difference in internal condition odds was detected between steelhead with moderate and severe external signs of disease ($P = 0.718$). Descaling was also associated with internal condition; the odds of having an internal condition for steelhead with 5–20% descaling was 2.4 times greater than steelhead with less than 5% descaling (95% CI: 1.0–5.7, $P = 0.057$). Similarly, steelhead with more than 20% descaling had odds of testing positive for an internal condition that were 3.3 times greater than those for steelhead with less than 5% descaling (95% CI: 1.2–9.0, $P = 0.020$). No difference in internal condition odds was detected between steelhead with 5–20% descaling and greater than 20% descaling ($P = 0.449$). After accounting for other measures of external condition, run stage, and rearing type, body injuries, ectoparasites, and fin damage, as measured in this study, were not significantly associated with internal condition (Table 3). Additionally, after accounting for external conditions, no differences in internal condition were detected between rearing types ($P = 0.323$) or among different run timings ($P = 0.122$).

TABLE 3. Odds ratios for the associations between measures of external condition and the occurrence of an infection in juvenile steelhead collected at Lower Monumental Dam in 2008 ($n = 222$). Infections included one or more of the following: mycotic organisms, trematodes, gill amoebae, *R. salmoninarum*, and infectious hematopoietic necrosis virus. Bold italics indicate model factors that were significant ($P \leq 0.05$).

Comparison[a]	Odds ratio	95% CI	*P*
Body injury			
Moderate versus absent	0.70	0.29–1.69	0.427
Severe versus absent	0.96	0.39–2.37	0.927
Severe versus moderate	1.37	0.47–4.03	0.567
Descaling			
5–20% versus <5%	2.35	0.97–5.69	0.057
>20% versus <5%	***3.30***	***1.20–9.04***	***0.020***
>20% versus 5–20%	1.40	0.59–3.35	0.449
Diseased			
Moderate versus absent	***24.33***	***2.47–239.89***	***0.006***
Severe versus absent	***39.17***	***10.01–153.26***	***<0.001***
Severe versus moderate	1.61	0.12–21.32	0.718
Fin damage			
Moderate versus absent	1.02	0.32–3.26	0.972
Severe versus absent	1.10	0.32–3.78	0.876
Severe versus moderate	1.08	0.50–2.35	0.847
Ectoparasites			
Moderate versus absent	0.96	0.13–7.16	0.967
Severe versus absent	0.00	0.00–∞	0.986
Severe versus moderate	0.00	0.00–∞	0.977
Integrated condition			
Fair versus good	0.90	0.26–3.12	0.866
Poor versus good	***5.61***	***1.76–17.94***	***0.004***
Poor versus fair	***6.24***	***1.95–20.00***	***0.002***

[a]See Table 1 for descriptions of external conditions.

Survival

Survival results indicated that external fish condition was associated with steelhead survival probability during 2007–2009 after accounting for migration year, run stage, FL, and rearing type in both survival and detection probability models (Tables 4, A.1). Since several external conditions were significantly associated with reductions in survival, results are primarily discussed through odds ratios addressing the significance of each specific external condition. The following results for estimated survival probabilities are presented in Figure 2.

Overall, the highest out-migration survival was associated with steelhead classified in excellent condition, with lower survival rates for steelhead in fair condition and the lowest ones for steelhead in poor condition. Specific estimates for integrated condition ranks indicated that the odds of survival for steelhead classified in poor condition were 1.4 times (95% CI: 1.3–1.6, $P < 0.001$) and 1.7 times (95% CI: 1.3–2.1, $P < 0.001$) lower than those for steelhead in good condition for short-distance and long-distance migrations, respectively (Table 4). Similarly, long-distance survival odds for steelhead in fair condition were 1.2 times lower than for steelhead in good condition (95% CI: 1.0–1.3, $P = 0.020$), although there appeared to be no difference between these two groups in short-distance survival (95% CI: 1.0–1.1, $P = 0.334$; Table 4). Short-distance and long-distance survival odds for steelhead in poor condition were both 1.4 times lower than steelhead in fair condition (95% CI: 1.2–1.5, $P < 0.001$ and 95% CI: 1.1–1.8, $P = 0.008$, respectively; Table 4).

Specific measures of external condition associated with reductions in survival odds included external signs of disease, descaling, and severe fin damage (Table 4). Steelhead with moderate signs of disease had short-distance and long-distance survival odds that were 2.7 times (95% CI: 2.0–3.8, $P < 0.001$) and 5.7 times (95% CI: 2.4–13.9, $P < 0.001$) lower than those for

TABLE 4. Odds ratios for the associations between measures of external condition and the estimated decrease in survival over short (Lower Monumental Dam to McNary Dam) and long distances (Lower Monumental Dam to Bonneville Dam) for juvenile steelhead collected at Lower Monumental Dam in 2007–2009 (n = 22,451). Decreases in survival were estimated after accounting for migration year (2007, 2008, or 2009), run stage (early, peak, or late), rearing type (hatchery or wild), and fork length in survival and detection probability models. Bold italics indicate model factors that were significant ($P \leq 0.05$).

	Decrease in survival					
	Short distance			Long distance		
Comparison[a]	Odds ratio	95% CI	P	Odds ratio	95% CI	P
Body injury						
Moderate versus absent	1.01	0.90–1.13	0.905	1.18	0.95–1.47	0.124
Severe versus absent	1.05	0.91–1.20	0.534	1.08	0.83–1.40	0.579
Severe versus moderate	1.04	0.88–1.23	0.660	0.91	0.66–1.25	0.581
Descaling						
5–20% versus <5%	***1.09***	***1.01–1.19***	***0.033***	1.16	1.00–1.35	0.057
>20% versus <5%	1.17	0.96–1.44	0.123	***1.58***	***1.03–2.40***	***0.035***
>20% versus 5–20%	1.07	0.87–1.32	0.499	1.36	0.89–2.08	0.160
Diseased						
Moderate versus absent	***2.70***	***1.95–3.75***	***<0.001***	***5.72***	***2.37–13.85***	***<0.001***
Severe versus absent	***3.56***	***2.61–4.86***	***<0.001***	***4.86***	***2.41–9.78***	***<0.001***
Severe versus moderate	1.32	0.86–2.03	0.208	0.85	0.28–2.54	0.770
Fin damage						
Moderate versus absent	0.97	0.88–1.07	0.512	0.98	0.82–1.17	0.805
Severe versus absent	1.05	0.94–1.19	0.391	***1.27***	***1.01–1.59***	***0.041***
Severe versus moderate	1.09	0.99–1.19	0.077	***1.30***	***1.09–1.55***	***0.004***
Ectoparasites						
Moderate versus absent	1.11	0.88–1.41	0.384	1.28	0.80–2.04	0.310
Severe versus absent	0.99	0.65–1.51	0.965	0.85	0.42–1.72	0.657
Severe versus moderate	0.89	0.56–1.43	0.631	0.67	0.29–1.53	0.338
Integrated condition						
Fair versus good	1.04	0.96–1.12	0.333	***1.21***	***1.03–1.41***	***0.020***
Poor versus good	***1.42***	***1.27–1.58***	***<0.001***	***1.67***	***1.33–2.08***	***<0.001***
Poor versus fair	***1.37***	***1.21–1.53***	***<0.001***	***1.38***	***1.09–1.76***	***0.008***

[a]See Table 1 for description of external conditions.

steelhead without disease signs, respectively. Similarly, steelhead with severe external signs of disease had short-distance and long-distance survival odds that were 3.6 times (95% CI: 2.6–4.9, $P < 0.001$) and 4.9 times (95% CI: 2.4–9.8, $P < 0.001$) lower than those for steelhead without disease signs, respectively. Steelhead with 5–20% descaling had short-distance and long-distance survival odds that were 1.1 times (95% CI: 1.0–1.2, $P = 0.033$) and 1.2 times (95% CI: 1.0–1.4, $P = 0.057$) lower than those for steelhead with less than 5% descaling, respectively. As descaling increased, survival odds further decreased; steelhead with greater than 20% descaling had long-distance survival odds that were 1.6 times lower than those for steelhead with less than 5% descaling (95% CI: 1.0–2.4, $P = 0.035$), although the difference between steelhead with more than 20% descaling and those with 5–20% descaling was not significant ($P = 0.160$; Table 4). Severe fin damage was associated with long-distance survival odds that were 1.3 times lower than those for steelhead without fin damage (95% CI: 1.0–1.6, $P = 0.041$), and also 1.3 times lower than those for steelhead with moderate fin damage (95% CI: 1.1–1.6, $P = 0.004$; Table 4). Finally, after accounting for other variables in the model, ectoparasites and body injuries, as measured in this study, were not significantly associated with decreased survival probabilities for either short-distance or long-distance migration (Table 4). Specific parameter estimates for all external conditions and nonexternal condition variables (FL, rearing type, run stage, and migration year) controlled for in this study are presented in Table A.1.

To further evaluate and interpret survival results, we plotted the survival estimates (with 95% CIs) associated with each of the external condition measures. Plotted values are presented for hatchery steelhead (majority of run) of average length (219 mm) that migrated during the peak run stage (majority of run) in 2009 (highest long-distance survival; Figure 2). Evaluating results in this manner further aided in our assessment of the biological significance of relationships between steelhead external conditions and survival. For instance, 5–20% descaling was associated with short-distance survival odds that were only 1.1

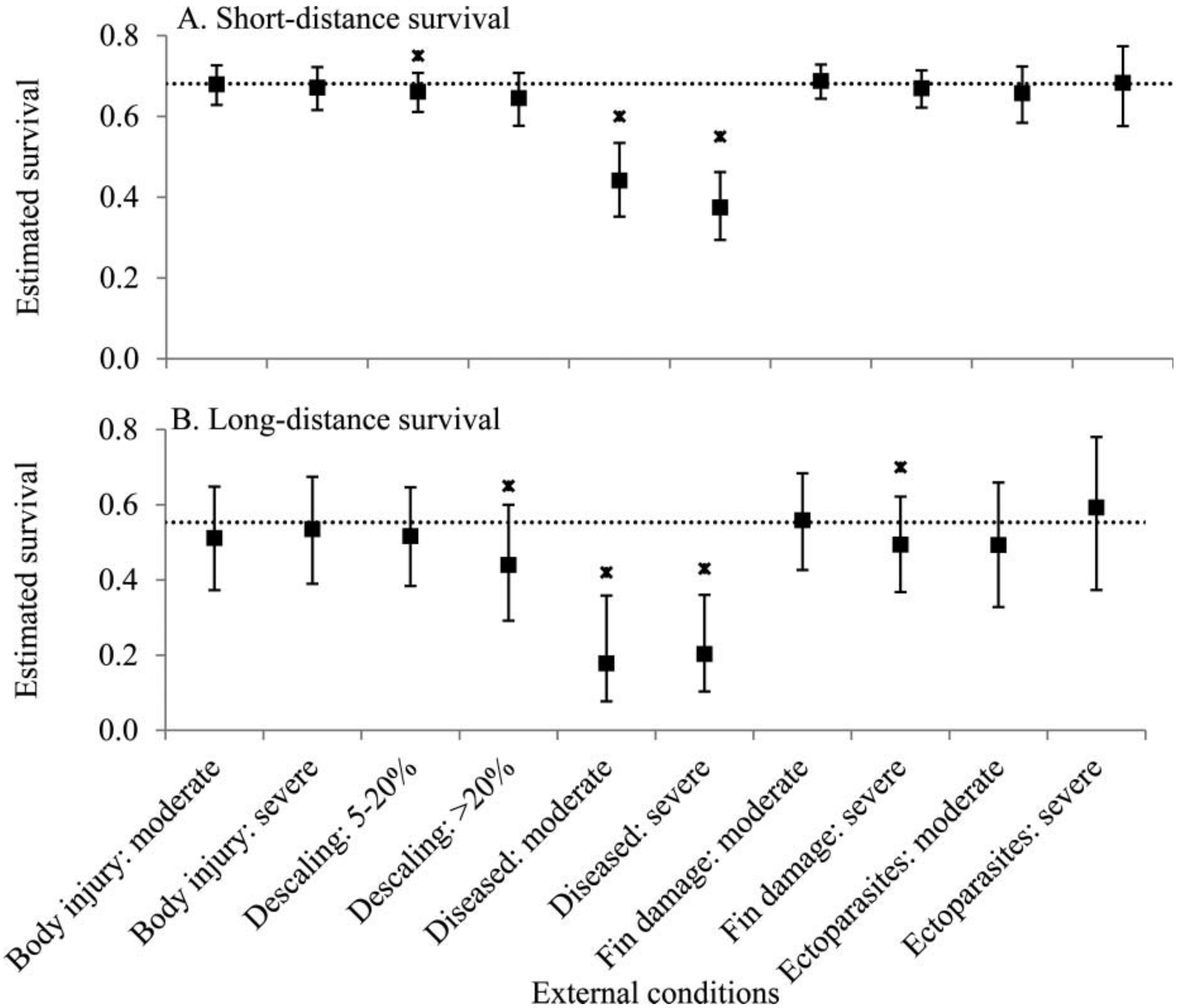

FIGURE 2. Estimated mean survival probabilities (error bars = 95% confidence intervals) for PIT-tagged juvenile steelhead from their release at Lower Monumental Dam to **(A)** McNary Dam (~119 river kilometers [rkm]) or **(B)** Bonneville Dam (~354 rkm). The dashed line represents mean survival probability when all measures of external conditions were classified as absent. External condition parameters associated with significant ($P < 0.05$) reductions in survival odds are denoted by asterisks. The estimates shown were calculated with other variables in the model being held constant, including migration year (2009), run stage (peak), rearing type (hatchery), and length (219 mm [mean length]).

times lower than those for steelhead with less than 5% descaling (95% CI: 1.0–1.2 times lower, $P = 0.033$). Once plotted, differences in short-distance survival probabilities between steelhead with 5–20% descaling ($\bar{x} = 0.66$, 95% CI: 0.61–0.71) and steelhead with less than 5% descaling ($\bar{x} = 0.68$, 95% CI: 0.63–0.72) became less obvious and may not be biologically important (Figure 2a). Differences, however, become more pronounced for long-distance survival probabilities (Figure 2b). Similarly, parameter estimates for moderate or severe external signs of disease indicated these conditions were associated with significant reductions in long-distance survival odds (Table 4). In this case, results indicated that 55% (95% CI: 42–68%) of hatchery steelhead without external signs of disease that migrated during the peak run stage in 2009 survived to Bonneville Dam. Conversely, only 18% (95% CI: 8–36%) and 20% (95% CI: 10–36%) of hatchery steelhead with moderate or severe external signs of disease survived to Bonneville Dam during that same time period, respectively (Figure 2b).

DISCUSSION

This study found that the external condition of out-migrating steelhead smolts (e.g., external signs of disease, descaling, severe fin damage, and the integrated condition rank) was associated with the internal condition and juvenile survival. Conversely, body injuries and ectoparasite infestations were not associated with internal condition or decreased juvenile survival after accounting for changes in other measures of external condition, run timing, and rearing type. These results suggest that external signs of disease, descaling, and severe fin damage were associated with reduced performance and that fish exhibiting these external measures were in poorer condition than fish without these conditions. These findings support the hypothesis that the external condition of a fish, as measured by a rapid, nondestructive technique, is correlated with relative differences in internal condition and survival of migrating salmonid smolts.

Although the external condition of fish is routinely used as part of an overall health index (e.g., Goede and Barton 1990), the direct associations among various external fish conditions and internal condition or survival have received relatively little attention. Direct and indirect effects from degraded external condition have previously been associated with decreased survival (Kostecki et al. 1987; Keefer et al. 2008) and decreased immunocompetence (Peters et al. 1988; Arkoosh 2006). This study corroborates these previous conclusions and demonstrates that fish exhibiting external trauma often experience reductions in multiple performance metrics.

Previous studies have found that pathogenic infections may reduce a fish's swimming ability (Swanson et al. 2002; Kocan et al. 2009) and survival probability (Morgan and Roberts 1976; Kocan et al. 2009). The five metrics used in the classification of internal condition (presence of mycotic organisms, trematodes, gill amoebae, *R. salmoninarum*, or IHNV) were found at a higher prevalence in steelhead with external signs of disease and descaling. Mechanisms contributing to increased infection occurrence may include changes to the skin, scale, and mucus complex of fish, which performs a number of functions including protection from pathogens and maintenance of homeostasis (Van Oosten 1957; Gadomski et al. 1994; Zydlewski et al. 2010). Kostecki et al. (1987) found that scale loss, although associated with decreased survival, was not the sole cause of death as descaling was also associated with internal injuries. Instead of direct causality between external conditions and survival, decreased survival may be due in part to a disruption of internal physiological processes (i.e., circulation, respiration, or osmoregulation; Bouck and Smith 1979; Schreck 1990), which were outwardly observed as degraded external condition.

An increasing number of studies suggest that individual fish characteristics, including external conditions, are important variables with respect to salmonid survival (Kostecki et al. 1987; Mesa et al. 1994; Zabel et al. 2005; Keefer et al. 2008). In this study, two external conditions were associated with both reduced survival and increased occurrence of an internal condition (external disease symptoms and descaling). The observational nature of this study made direct correlations and causality difficult to fully resolve. For instance, there were no control groups, all steelhead evaluated for internal conditions were sacrificed, and potentially important explanatory variables went unmeasured (e.g., stressors experienced earlier in life). Statistical results from this study should therefore not be used to infer causality, but are useful in identifying broad patterns in the data. In the end, the use of external measures of condition is not meant to be diagnostic, but instead provides a useful indicator of sublethal pathologies or other performance metrics (e.g., survival) through a technique that is quick, minimally invasive, and nonlethal.

The results of this study indicate that monitoring and assessing external fish condition at the level of individual fish can be used to demonstrate correlations with various health indices and survival at both the individual and population levels. In addition to external measures of condition, other individual characteristics, such as length, weight, or rearing type (hatchery or wild) can easily be incorporated to create a unique profile for each fish. Although not the focus of this paper, results associating survival and nonexternal condition variables (Table A.1) were consistent with previously published studies that have indicated juvenile steelhead survival and detection probability in the Columbia River basin can be influenced by individual fish characteristics (e.g., FL, Zabel et al. 2005) and environmental conditions (e.g., run timing or migration year, Skalski 1998; Muir et al. 2001; Plumb et al. 2006). Overall, a growing body of evidence indicates that incorporating individual fish characteristics into population monitoring programs can lead to an increased understanding of salmonid population dynamics and phenotypic traits associated with survival of ESA-listed salmonids.

This study demonstrated that external condition, as measured by a rapid, nonlethal external examination, provides insight into the health and survival of migrating juvenile steelhead under various environmental conditions. Assessing the condition of fish in a nonlethal manner can be particularly important when working with species and populations that are listed as threatened or endangered. In this study, about 48% (10,790 of 22,451) of juvenile steelhead sampled at LMN Dam in 2007, 2008, and 2009 possessed at least one of the three external conditions associated with decreased survival (external signs of disease, more than 5% descaling, and severe fin damage). Additionally, prevalence of external conditions recorded at LMN Dam may not fully represent the prevalence of these conditions in the general population of out-migrating smolts as a disproportionate percentage of diseased or injured steelhead may have died before reaching LMN Dam. Increased mortality of diseased or injured steelhead before their arrival at LMN Dam would imply that these conditions may be more prevalent and play a more important role in juvenile steelhead mortality than the results from this study suggest. Coordination of efforts to record the prevalence of various external conditions across sampling locations within the Columbia River basin could be used to validate the use of external condition measures as a metric for juvenile salmonid health and survival.

In smolts, the highest out-migration survival typically occurs when physiological changes coincide with optimum environmental conditions (e.g., temperature and flow; McCormick et al. 1998). Condition-dependent mortality has previously been documented in other salmonid life stages (Keefer et al. 2008). The effects of sublethal pathologies and reduced performance detected in out-migrating smolts could also persist over periods longer than studied here, as some conditions may not affect survival until a later life stage. These long-term effects are of particular concern as steelhead are exposed to a host of additional stressors in the estuary and ocean that were not evaluated by this study (e.g., increased salinity, predation, and others). Improvements to fish passage that allow juvenile salmonids to successfully navigate the hydrosystem with minimal additional stress and allostatic load (McEwen and Stellar 1993) could enhance salmonid survival through the hydrosystem and possibly reduce delayed mortality after exiting the hydrosystem (Schreck et al. 2006).

Ultimately, the probability of an individual fish's surviving the juvenile life stage is determined by a complex set of interacting factors, including individual fish characteristics and environmental conditions (Skalski 1998; Muir et al. 2001; Zabel et al. 2005; Plumb et al. 2006). Nonlethal external examinations were, however, able to identify several external conditions that were correlated with internal condition and decreased juvenile survival during in-river out-migration. Evaluating fish health status based solely on external criteria is advantageous with respect to minimizing fish mortality, speed of evaluation, uniformity in technique, cost, and an ability to relate fish condition to postrelease behavior, movements, and survival. Methods that help indentify individual fish characteristics associated with decreased survival can become a valuable source of information for fisheries managers and population monitoring programs. In the future, and with additional research involving various salmonid ESUs, external examination techniques could hold promise as a reliable assessment of relative fish condition when lethal collection is not warranted or feasible.

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REFERENCES

Adams, S. M., editor. 1990. Biological indicators of stress in fish. American Fisheries Society, Symposium 8, Bethesda, Maryland.

Adams, S. M., A. M. Brown, and R. W. Goede. 1993. A quantitative health assessment index for rapid evaluation of fish condition in the field. Transactions of the American Fisheries Society 122:63–73.

Arkoosh, M. R., A. N. Kagley, B. F. Anulacion, D. A. Boylen, B. P. Sandford, F. J. Loge, L. L. Johnson, and T. K. Collier. 2006. Disease susceptibility of hatchery Snake River spring-summer Chinook salmon with different juvenile migration histories in the Columbia River. Journal of Aquatic Animal Health 18:223–231.

Bancroft, J. D., and A. Stevens. 1994. Manual of histological techniques and their diagnostic applications, 2nd edition. Churchill Livingstone, Edinburgh, UK.

Barton, B. A., J. D. Morgan, and M. M. Vijayan. 2002. Physiological and condition-related indicators of environmental stress in fish. Pages 111–148 *in* S. M. Adams, editor. Biological indicators of aquatic ecosystem stress. American Fisheries Society, Bethesda, Maryland.

Bouck, G. R., and S. D. Smith. 1979. Mortality of experimentally descaled smolts of coho salmon (*Oncorhynchus kisutch*) in fresh and salt water. Transactions of the American Fisheries Society 108:67–69.

Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22:35–51.

Chase, D. M., and R. J. Pascho. 1998. Development of a nested polymerase chain reaction for amplification of a sequence of the p57 gene of *Renibacterium salmoninarum* that provides a highly sensitive method for detection of the bacterium in salmonid kidney. Diseases of Aquatic Organisms 34: 223–229.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429–438.

Del Cerro, A., I. Marquez, and J. A. Guijarro. 2002. Simultaneous detection of *Aeromonas salmonicida*, *Flavobacterium psychrophilum*, and *Yersinia ruckeri*, three major fish pathogens, by multiplex PCR. Applied and Environmental Microbiology 68:5177–5180.

Dieguez-Uribeondo, J., J. M. Fregeneda-Grandes, L. Cerenius, E. Perez-Injesta, J. M. Aller-Gancedo, M. T. Telleria, K. Soderhall, and M. P. Martin. 2007. Reevaluation of the enigmatic species complex *Saprolegnia diclina-Saprolegnia parasitica* based on morphological, physiological, and molecular data. Fungal Genetics and Biology 44:585–601.

Dorsch, M., N. J. Ashbolt, P. T. Cox, and A. E. Goodman. 1994. Rapid identification of Aeromonas species using 16s rDNA targeted oligonucleotide primers: a molecular approach based on screening of environmental isolates. Journal of Applied Microbiology 77:722–726.

Erickson, D. G., and F. G. Wallace. 1959. Studies on blood flukes of the genus *Sanguinicola*. Journal of Parasitology 45:310–32.

Evans, A. F., R. E. Beaty, M. S. Fitzpatrick, and K. Collis. 2004. Identification and enumeration of steelhead kelts at a Snake River hydroelectric dam. Transactions of the American Fisheries Society 133:1089–1099.

FPC (Fish Passage Center). 2010. Fish passage center of the Columbia Basin fish and wildlife authority. Available: www.fpc.org. (February 2010).

Gadomski, D. M., M. G. Mesa, and T. M. Olson. 1994. Vulnerability to predation and physiological stress responses of experimentally descaled juvenile Chinook salmon, (*Oncorhynchus tshawytscha*). Environmental Biology of Fishes 39:191–199.

Goede, R. W., and B. A. Barton. 1990. Organismic indices and an autopsy-based assessment as indicators of health and condition of fish. Pages 93–108 *in* S. Marshall Adams, editor. Biological indicators of stress in fish. American Fisheries Society, Symposium 8, Bethesda, Maryland.

Good, T. P., R. S. Waples, and P. Admas, editors. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Technical Memorandum NMFS-NWFSC-66:598.

Hoffman, G. L. 1999. Parasites of North American freshwater fishes, 2nd edition. Cornell University Press, Ithaca, New York.

Hong, G. E., D. G. Kim, J. Y. Bae, S. H. Ahn, S. C. Bai, and I. S. Kong. 2007. Species-specific PCR detection of the fish pathogen, *Vibrio anguillarum*, using the amiB gene, which encodes N-acetylmuramoyl-L-alanine amidase. FEMS (Federation of European Microbiological Societies) Microbiology Letters 269:201–206.

Hopwood, D. 1990. Fixation and fixatives. Pages 21–42 *in* J. D. Bancroft and A. Stevens, editors. Theory and practice of histological techniques. Churchill Livingstone, Edinburgh, UK.

Hosmer, D. W. Jr., and S. Lemeshow. 2000. Applied logistic regression, 2nd edition. Wiley, New York.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225–247.

Keefer, M. L., R. H. Wertheimer, A. F. Evans, C. T. Boggs, and C. A. Peery. 2008. Iteroparity in Columbia River summer-run steelhead (*Oncorhynchus mykiss*): implications for conservation. Canadian Journal of Fisheries and Aquatic Sciences 65:2592–2605.

Kocan, R., P. Hershberger, G. Sanders, and J. Winton. 2009. Effects of temperature on disease progression and swimming stamina in *Ichthyophonus*-infected rainbow trout, *Oncorhynchus mykiss* (Walbaum). Journal of Fish Diseases 32:835–843.

Kostecki, T., P. Clifford, S. P. Gloss, and J. C. Carlisle. 1987. Scale loss and survival in smolts of Atlantic salmon (*Salmo salar*) after turbine passage. Canadian Journal of Fisheries and Aquatic Sciences 44:210–214.

Ledgerwood, R. D., B. A. Ryan, E. M. Dawley, E. P. Nunnallee, and J. W. Ferguson. 2004. A surface trawl to detect migrating juvenile salmonids tagged with passive integrated transponder tags. North American Journal of Fisheries Management 24:440–451.

McCormick, S. D., L. P. Hansen, T. P. Quinn, and R. L. Saunders. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55:77–92.

McEwen, B. S., and E. Stellar. 1993. Stress and the individual: mechanisms leading to disease. Archives of Internal Medicine 153:2093–2101.

Mesa, M. G. 1994. Effects of multiple acute stressors on the predator avoidance ability and physiology of juvenile Chinook salmon. Transactions of the American Fisheries Society 123:786–793.

Mesa, M. G., P. P. Thomas, M. G. Dena, and H. P. James. 1994. Are all prey created equal? A review and synthesis of differential predation on prey in substandard condition. Journal of Fish Biology 45:81–96.

Morgan, R. I. G., and R. J. Roberts. 1976. The histopathology of salmon tagging: IV. The effect of severe exercise on the induced tagging lesion in salmon parr at two temperatures. Journal of Fish Biology 8:289–292.

Muir, W. D., S. G. Smith, J. G. Williams, E. E. Hockersmith, and J. R. Skalski. 2001. Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia Rivers. North American Journal of Fisheries Management 21:269–282.

Neff, J. M. 1985. Use of biochemical measurements to detect pollutant-mediated damage to fish. Pages 155–183 *in* R. D. Cardwell, R. Purdy, and R. C. Bahner, editors. Aquatic toxicology and hazard assessment. American Society for Testing Materials, Philadelphia.

Nielson, L. A. 1992. Methods for marking fish and shellfish. American Fisheries Society, Special Publication 23, Bethesda, Maryland.

Niimi, A. J. 1990. Review of biochemical methods and other indicators to assess fish health in aquatic ecosystems containing toxic chemicals. Journal of Great Lakes Research 16:529–541.

Noga, E. J. 1996. Fish disease: diagnosis and treatment. Mosby-Year Book, St. Louis, Missouri.

Olla, B. L., M. W. Davis, and C. B. Schreck. 1992. Comparison of predator avoidance capabilities with corticosteroid levels induced by stress in juvenile coho salmon. Transactions of the American Fisheries Society 121: 544–547.

Peters, G., M. Faisal, T. Lang, and A. Iman. 1988. Stress caused by social interaction and its effect on susceptibility to *Aeromonas hydrophila* infection in rainbow trout (*Salmo gairdneri*). Diseases of Aquatic Organisms 4: 83–89.

Pickering, A. D. 1993. Endocrine-induced pathology in stressed salmonid fish. Fisheries Research 17:35–50.

Plumb, J. M., R. W. Perry, N. S. Adams, and D. W. Rondorf. 2006. The effects of river impoundment and hatchery rearing on the migration behavior of juvenile steelhead in the Lower Snake River, Washington. North American Journal of Fisheries Management 26:438–452.

Prentice, E. F., T. A. Flagg, and C. S. McCutcheon. 1990a. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Pages 317–322 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, and D. F. Brastow. 1990b. PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. Pages 323–334 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, D. F. Brastow, and D. C. Cross. 1990c. Equipment, methods and an automated data-entry station for PIT tagging. Pages 335–340 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Presnell, J. K., and M. P. Schreibman. 1997. Humason's animal tissue techniques, 5th edition. Johns Hopkins University Press, Baltimore, Maryland.

Schreck, C. B. 1990. Physiological, behavioral and performance indicators of stress. Pages 29–37 *in* S. M. Adams, editor. Biological indicators of stress in fish. American Fisheries Society, Symposium 8, Bethesda, Maryland.

Schreck, C. B., T. P. Stahl, L. E. Davis, D. D. Roby, and B. J. Clemens. 2006. Mortality estimates of juvenile spring-summer Chinook salmon in the lower Columbia River and estuary, 1992–1998: evidence for delayed mortality? Transactions of the American Fisheries Society 135:457–475.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52:249–259.

Skalski, J. R. 1998. Estimating season-wide survival rates of outmigrating salmon smolt in the Snake River, Washington. Canadian Journal of Fisheries and Aquatic Sciences 55:761–769.

Swanson, C., D. V. Baxa, P. S. Young, J. J. Cech Jr., and R. P. Hedrick. 2002. Reduced swimming performance in delta smelt infected with *Mycobacterium* spp. Journal of Fish Biology 61:1012–1020.

Van Oosten, J. 1957. The skin and scales. Pages 207–244 *in* M. E. Brown, editor. The physiology of fishes. Academic Press, New York.

Waples, R. S. 1991. Definition of "species" under the Endangered Species Act: application to Pacific salmon. NOAA Technical Memorandum NMFS-NWFSC-194.

Wedemeyer, G. A., D. J. McLeay, and C. P. Goodyear. 1984. Assessing the tolerance of fish and fish populations to environmental stress: the problems and methods of monitoring. Pages 163–195 *in* V. W. Cairns, P. V. Hodson, and J. O. Nriagu, editors. Contamination effects on fisheries. Wiley, New York.

Welker, T. L., C. A. Shoemaker, C. R. Arias, and P. H. Klesius. 2005. Transmission and detection of *Flavobacterium columnare* in channel catfish *Ictalurus punctatus*. Diseases of Aquatic Organisms 63:129–138.

Wendelaar Bonga, S. E. 1997. The stress response in fish. Physiological Reviews 77:591–625.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

Williams, K., S. Blake, A. Sweeney, J. T. Singer, and B. L. Nicholson. 1999. Multiplex reverse transcriptase PCR assay for simultaneous detection of three fish viruses. Journal of Clinical Microbiology 37:4139–4141.

Zabel, R. W., T. Wagner, J. L. Congleton, S. G. Smith, and J. G. Williams. 2005. Survival and selection of migrating salmon from capture-recapture models with individual traits. Ecological Applications 15:1427–1439.

Zydlewski, J., G. Zydlewski, and G. R. Danner. 2010. Descaling injury impairs the osmoregulatory ability of Atlantic salmon smolts entering seawater. Transactions of the American Fisheries Society 139:129–136.

Appendix: Supplemental Information Relating External Condition and Pathogen Presence in Steelhead to Out-Migration Survival

TABLE A.1. Survival (φ) and detection probability (*p*) regression coefficients (beta) and SE values from a model predicting juvenile steelhead short-distance (Lower Monumental Dam to McNary Dam) and long-distance survival (Lower Monumental Dam to Bonneville Dam). Regression coefficient *P*-values for categorical data are based on comparisons with set reference levels (migration year = 2007, run stage = early, rearing type = wild-reared, all external conditions absent); positive regression coefficients are associated with increases in survival or detection probability and negative regression coefficients with decreases in survival or detection probability. See Methods for variable descriptions.

	Short-distance survival			Long-distance survival		
Model factor	Beta	SE	*P*	Beta	SE	*P*
φ Intercept	–1.600	0.196	< 0.001	–3.156	0.350	< 0.001
φ Body injury: moderate	–0.007	0.057	0.905	–0.168	0.109	0.124
φ Body injury: severe	–0.044	0.071	0.534	–0.074	0.134	0.579
φ Descaling: 5–20%	–0.090	0.042	0.033	–0.149	0.078	0.057
φ Descaling: >20%	–0.160	0.104	0.123	–0.455	0.215	0.035
φ Diseased: moderate	–0.993	0.167	< 0.001	–1.745	0.451	< 0.001
φ Diseased: severe	–1.270	0.158	< 0.001	–1.581	0.357	< 0.001
φ Fin damage: moderate	0.032	0.049	0.512	0.023	0.092	0.805
φ Fin damage: severe	–0.052	0.061	0.391	–0.237	0.116	0.041
φ Ectoparasites: moderate	–0.106	0.122	0.384	–0.243	0.240	0.310
φ Ectoparasites: severe	0.009	0.214	0.965	0.160	0.360	0.657
φ Survival location	1.001	0.230	< 0.001	3.468	0.374	< 0.001
φ Migration year: 2008	0.428	0.079	< 0.001	0.170	0.125	0.175
φ Migration year: 2009	0.103	0.081	0.202	0.327	0.122	0.007
φ Migration period: peak	–0.304	0.053	< 0.001	–0.070	0.105	0.507
φ Migration period: late	–0.775	0.061	< 0.001	–0.261	0.121	0.030
φ Fork length (mm)	0.008	0.002	< 0.001	–0.002	0.002	0.366
φ Rearing: hatchery reared	–0.135	0.074	0.068	–0.013	0.149	0.933
p Intercept	2.351	0.411	< 0.001	5.695	50.499	0.910
p Detection location	–2.214	0.406	< 0.001	–9.697	50.481	0.848
p Migration year: 2008	0.063	0.086	0.467	0.557	0.121	< 0.001
p Migration year: 2009	0.671	0.078	< 0.001	0.501	0.114	< 0.001
p Migration period: peak	–0.206	0.068	0.003	–0.501	0.099	< 0.001
p Migration period: late	–0.368	0.080	< 0.001	–0.856	0.117	< 0.001
p Fork length (mm)	–0.007	0.001	< 0.001	0.012	0.002	< 0.001
p Rearing: hatchery reared	–0.045	0.088	0.613	–0.141	0.132	0.286

TABLE A.2. Occurrence of external measures of condition in steelhead captured at Lower Monumental Dam in 2007, 2008, and 2009 ($n = 22{,}451$). See Methods for additional information.

Condition measure		Body injuries			Descaling			External disease signs			Fin damage			Ectoparasites		
	Occurrence	Absent	Moderate	Severe	<5%	5–20%	>20%	Absent	Moderate	Severe	Absent	Moderate	Severe	Absent	Moderate	Severe
Body injuries	Absent	18,151	0	0	12,544	5,168	439	17,594	256	301	4,369	10,136	3,646	17,610	408	133
	Moderate		2,609	0	1,369	1,027	213	2,505	42	62	476	1,514	619	2,567	33	9
	Severe			1,691	921	596	174	1,502	25	164	293	928	470	1,651	25	15
Descaling	<5%				14,834	0	0	14,436	171	227	4,103	7,835	2,896	14,331	367	136
	5–20%					6,791	0	6,409	137	245	957	4,234	1,600	6,689	85	17
	>20%						826	756	15	55	78	509	239	808	14	4
External disease signs	Absent							21,601	0	0	5,015	12,142	4,444	20,990	456	155
	Moderate								323	0	59	188	76	317	6	0
	Severe									527	64	248	215	521	4	2
Fin damage	Absent										5,138	0	0	4,803	237	98
	Moderate											12,578	0	12339	186	53
	Severe												4,735	4,686	43	6
Ectoparasites	Absent													21,828	0	0
	Moderate														466	0
	Severe															157