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ARTICLE

Life History Diversity of Snake River Steelhead Populations between and within Management Categories

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Abstract
Grouping populations for management may overlook the fine-scale diversity underpinning the stability and resilience of meta-populations and fisheries. A bimodal timing distribution of summer-run steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) historically was observed at Bonneville Dam (BON), the first barrier to upstream migration in the Columbia River basin. Early mode fish (A-run) tended to be younger and smaller (<78 cm) than later fish (B-run). While A-run fish spawn throughout the Columbia River basin, B-run fish spawn primarily in the Snake River basin. Managers used indices of these modes to make fishery decisions, and later these criteria were adopted for conservation. It is still unclear how life history and body size differences among wild Snake River populations are related to the categories at BON. We examined population parameters characterizing the two categories (date of passage at BON, length) and parameters directly affecting population dynamics (age composition, sex ratio). The life history portfolio of Snake River steelhead is quite diverse. There was broad overlap among populations in several respects, forming a gradient in life history characteristics rather than a dichotomous break. All populations produced adults <78 cm and adults returning after August 25. Median lengths of putative B-run populations were close to the criterion that was supposed to be a defining characteristic. In contrast, few A-run populations produced many adults ≥78 cm. Mean percentage of two-ocean fish was 52.1% for A-run populations and 82.0% for B-run populations. Mean age at spawn was greater in populations producing older smolts. Sex ratio was female biased, and older populations had greater percentages of females. Although the run-type dichotomy was useful for management of fisheries in the past, it is not useful for conservation. A combination of genetic stock identification at main-stem dams and population-specific monitoring in natal streams provides a unified framework for the assessment of fisheries management and conservation objectives.

Differences in timing, size, sex ratio, and age composition among populations with migratory life histories are important to fisheries management. For example, salmon spawning runs are typically characterized by the season of freshwater entry, and riverine salmon fisheries are structured around run timing to harvest abundant stocks and protect weaker ones. Fisheries

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may be managed by run timing, but salmon spawning runs often are composed of diverse populations (e.g., Hilborn et al. 2003). Grouping populations into broad categories for conservation and fisheries management may overlook the fine-scale diversity underpinning the stability and resilience of metapopulations and fisheries (Braun et al. 2016).

Oncorhynchus mykiss has the most diverse life history repertoire of the Pacific salmonids (genus *Oncorhynchus*; Quinn 2005). Individuals may migrate to the ocean (steelhead [anadromous Rainbow Trout]) or remain in freshwater (Rainbow Trout or Redband Trout). Unlike most species of this genus, *O. mykiss* is capable of iteroparity, although infrequently in some steelhead populations (Busby et al. 1996). Furthermore, steelhead spend varying amounts of time in freshwater and saltwater habitats. Expression of anadromy is potentially influenced by factors affecting juvenile growth and survival, factors affecting survival to and in the ocean, and factors affecting adult spawning migration (Kendall et al. 2015). The decisions to migrate and mature apparently are threshold traits controlled by individual condition and adapted to the environment, allowing for flexibility in life history expression within and among populations (Thorpe et al. 1998; Sloat et al. 2014; Kendall et al. 2015). Theory suggests that anadromy confers greater fitness benefits for females than males because larger size increases fecundity in females while males have evolved behaviors that allow smaller individuals to successfully compete with larger ones (Hendry et al. 2004). Therefore, steelhead display a tremendous amount of variation in age and size at maturity, which results in a continuum of life histories that depends on the rearing environment and local selective pressures (Brannon et al. 2004). Variable expression of anadromy in populations of *O. mykiss* and the factors controlling that expression are of management interest because of the cultural, ecological, economic, and recreational values focused on steelhead.

Steelhead management in the Columbia River basin.—In the interior Columbia River basin (east of the Cascade Mountains), summer-run steelhead populations historically were managed as two stocks, termed A-run and B-run. The stocks were distinguished by run timing at Bonneville Dam (BON), the first dam encountered during the spawning migration (Robards and Quinn 2002; WDFW and ODFW 2002; Figure 1). The A-run steelhead passed BON on or before August 25 and were thought to spawn throughout the interior Columbia basin the following spring. The B-run steelhead passed BON after August 25 and were thought to spawn primarily in certain tributaries of the Snake River in Idaho the following spring (Idaho Department of Fish and Game [IDFG], 1994 documents submitted to the National Marine Fisheries Service for the U.S. Endangered Species Act [ESA] administrative record on West Coast steelhead). The A-run was composed of smaller individuals that typically spent 1 or 2 years at sea, whereas the B-run was composed of larger individuals that typically spent 2 or 3 years at sea (Busby et al. 1996). Managers used the date criterion (on or before August 25) to estimate spawning run sizes and make in-season fishery management decisions (WDFW and ODFW 2002). Both stocks are composed of multiple populations.

During the 1980s, changes in modal run timing created problems for steelhead managers evaluating hatchery programs and assessing the impact of main-stem Columbia River fisheries on wild stocks. Wild steelhead populations had declined, and the annual return became dominated by hatchery fish. Columbia basin hatchery steelhead stocks were developed from A-run stocks with one exception (North Fork Clearwater River stock). By the 1980s, the peak of the A-run had become later, such that the B-run mode was hard to distinguish (Robards and Quinn 2002).

The Columbia River steelhead management scheme was revised in 1999 because of the loss of distinction between the modes (ODFW and WDFW 2000). Steelhead passing BON from November 1 to March 31 were counted as winter-run steelhead, those passing BON from April 1 to June 30 were counted as summer-run fish bound for tributaries to Bonneville Pool, and those passing BON from July 1 to October 31 were counted as upriver summer-run fish (the majority of all steelhead). The upriver summer-run steelhead continued to be managed as two stocks (group A and group B) but now based on a length criterion. Current management classifies all upriver steelhead <78-cm FL as group A and those ≥78-cm FL as group B (ODFW and WDFW 2000). The abundances of all group-A and group-B steelhead and the abundances of wild fish in these groups are used to manage fisheries for steelhead and fall Chinook Salmon *O. tshawytscha* in the Columbia River downstream of the Snake River confluence. This scheme was deemed sufficient for fisheries management in the interim until better stock-specific information could be derived.

The conservation of wild Columbia River steelhead is also an important management concern. Historically, most summer-run steelhead in the Columbia River basin were from the Snake River (Mallett 1974). Spawning runs of wild Snake River steelhead declined precipitously in the early 1980s and recovered in the late 1980s. Abundance declined again with extreme lows through most of the 1990s. There was a substantial increase in the early 2000s, but abundance has continued to fluctuate since then (Ford et al. 2011). Snake River steelhead were listed as threatened under the ESA in 1997 (NMFS 1997). Status assessments conducted for the ESA require population-specific information, including life history diversity (McElhany et al. 2000). Because many steelhead in the Snake River spawn near the peak of the spring snowmelt in remote and rugged areas in Idaho, data on spawning wild steelhead in most populations were lacking. In the absence of more specific information, the Interior Columbia Technical Recovery Team (ICTRT; ICTRT 2009) adapted the Columbia River fisheries management scheme and classified each Snake River population as A-run or B-run. Status and

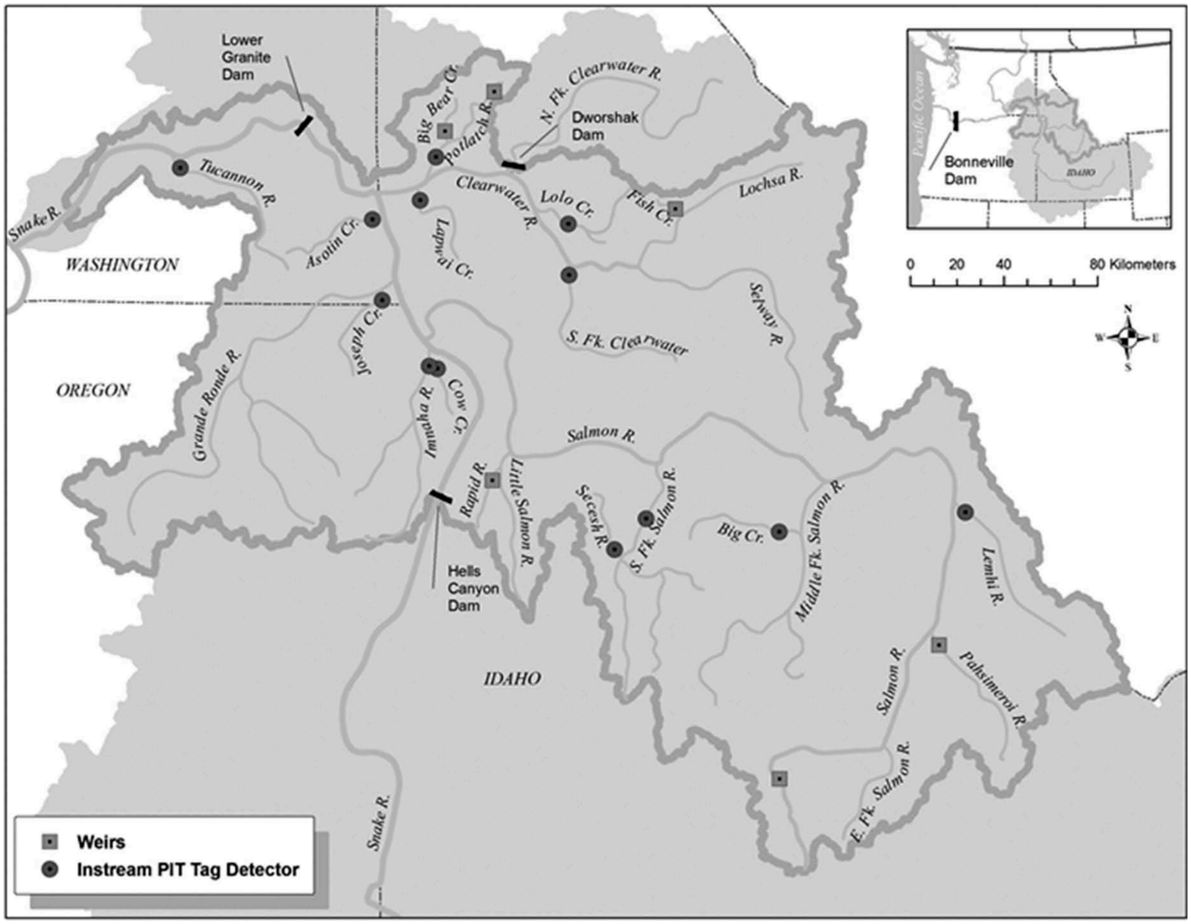

FIGURE 1. Locations of sampling infrastructure used to collect data for this study. Inset shows the Columbia River basin and the location of Bonneville Dam. Gray area is the Snake River basin.

viability assessments for Idaho steelhead populations were performed on an "average" population of each run type based on length-stratified counts of natural-origin steelhead at Lower Granite Dam (LGR), 695 km upstream from the Pacific Ocean on the Snake River (Figure 1) and were made assuming perfect discrimination by length and a common age structure within run type (ICTRT 2009).

It is still unclear how life history and body size differences observed in wild steelhead in the Snake River (at LGR and in spawning reaches) are related to the groups observed at BON (Busby et al. 1996). Indeed, the meaning of A or B differs if one is referring to steelhead of a certain size or if one is referring to steelhead from certain populations. To avoid confusion between the conservation classification and the fisheries management scheme, hereafter we use the terms "A-run" and "B-run" to refer to Snake River steelhead populations as defined by the ICTRT for ESA listing and recovery planning. The terms "group A" and "group B" refer to upriver summer-run steelhead in the Columbia River as defined by length in the 2008–2017 Management Agreement made under the provisions of U.S. v. Oregon (1969) for fisheries management downstream of the Snake River. Regardless of the intended meaning, theory and empirical results imply there should be some degree of overlap in the characteristics of the two categories, which could hinder achievement of management goals based on them.

The goal of this study was to investigate the diversity within and between the two categories used to manage wild Snake River steelhead, specifically in which life history aspects do the two groups overlap and in which are they distinct. We assembled recent life history data (spawning run years 2009–2010 through 2011–2012) from multiple populations and measured the degree to which each population conforms to the historic and current fisheries management classifications. We examined the population parameters thought to characterize the two categories (date at BON and FL) and the parameters expected to vary among steelhead populations that directly affect population dynamics (age composition and sex ratio). We expected a gradient of characteristic frequencies among the populations as described by Brannon et al. (2004). Describing and understanding this diversity is important to the conservation and management of these steelhead populations.

METHODS

We focused on wild Snake River steelhead populations or major spawning aggregates with sufficient data on returning adults to estimate the life history characteristics of interest. The most recent peaks in abundance of wild Snake River steelhead were spawning run years 2009–2010 through 2011–2012; we used these three spawning runs because they were most likely to yield sufficient data for the broadest range of populations. In the Snake River basin, B-run steelhead are thought to spawn in the upper tributaries of the Clearwater River and in the Middle and South forks of the Salmon River (IDFG, documents; Figure 1). Data for putative B-run steelhead populations were collected on fish from Big Creek, Fish Creek, Lolo Creek, Secesh River, South Fork Clearwater River, and South Fork Salmon River. Data for putative A-run steelhead populations were collected on fish from Asotin Creek, Imnaha River, Joseph Creek, Lapwai Creek, Lemhi River, Pahsimeroi River, Potlatch River, Rapid River, Tucannon River, and the upper Salmon River at Sawtooth Hatchery. These locations gave good coverage of the environmental conditions where steelhead spawn and rear in the Snake River basin.

Data collection.—Date of passage at BON was estimated based on the detection of wild adults that were tagged as juveniles emigrating from their natal tributary in the Snake River basin. Passive integrated transponder (PIT) tags emit a unique code when the tag passes through a magnetic field that can be read by a detector (Prentice et al. 1990). The fish ladder at BON contains vertical-slot detection systems that detect nearly 100% of PIT-tagged adult salmon migrating past the dam (Fryer et al. 2012). Rotary screw traps operate near the mouths of spawning tributaries through the ice-free season, and emigrating juveniles (≥80-mm FL in most locations) were tagged to estimate survival and trap efficiency. We assumed the tagged juveniles adequately represented the distribution of subsequent adult return dates across BON. Dates of first detection of adults crossing BON were obtained by querying the PTAGIS database (www.ptagis.org) for fish tagged in the selected tributaries. Furthermore, a systematic sample of steelhead smolts were tagged at the LGR juvenile fish facility as they emigrated downstream past the dam each spring. We performed a query for fish tagged as wild juveniles at LGR that were subsequently detected as adults in selected tributaries at weirs or instream PIT tag detectors (IPTDs) and used their dates of passage at BON in the analysis.

Samples and morphometric data were collected nonlethally from adult steelhead handled either at a weir located in a tributary, by angling (Big Creek only), or at the LGR adult trap (Figure 1). Wild adults sampled at LGR that were not carrying a PIT tag had one injected. Scale and tissue samples were collected from all tagged steelhead (Ackerman et al. 2012a, 2014). Natal tributary was identified by capture in the tributary or by detection at an IPTD between January 1 and May 31. If an adult fish was detected in more than one tributary, we assumed that the last detection was the spawning location. The South Fork Clearwater and Lolo Creek IPTDs were operational only during the 2011–2012 spawning run. The Asotin Creek, Joseph Creek, and Imnaha River IPTDs were operational during the 2010–2011 and 2011–2012 spawning runs. The weirs, angling surveys, LGR trap, and all other IPTDs were operational during all three spawning runs. Fork length was measured to the nearest whole centimeter. Freshwater and ocean ages were assigned based on scale examination (Wright et al. 2015). Total age at spawning is the sum of freshwater and ocean ages plus 1 for the winter spent in freshwater before spawning. Sex was determined using external morphology for fish collected at weirs or angling and using a genetic assay on tissue samples (Campbell et al. 2012) for fish sampled at LGR.

Data analysis.—The primary analysis investigated the diversity within each population with respect to the historic and current fisheries management criteria (date at BON, FL), and then evaluated the proportion of each population that would be classified into the opposite fishery management group (e.g., proportion of fish from Fish Creek classified as group A). We combined data from all three spawning runs for all analyses. To describe the central tendency and range of the length distribution of each population, we computed the median, fifth, and 95th percentiles of the observed FLs. We similarly characterized the adult return dates for each population using the median, fifth, and 95th percentiles of the day of arrival at BON. To visualize the diversity within and among the populations, we plotted the percentiles with respect to the length and date criteria. To evaluate the relationship of that diversity to the management criteria, we relied directly on the data in a manner that parallels how groups of steelhead are assessed in the management arena. For each population, we characterized the percentage of fish that would be classified as the opposing putative group at BON in two ways: (1) the percentages of the observed data that fall outside the current length criterion for each run type, and (2) the percentages of the observed data that fall outside the historic timing of the putative run type.

We also investigated trends in age composition and sex ratio among the populations. For each population, we reported the percentage of adults by freshwater and ocean age, the mean total age at spawning, and the percentage of females. We contrasted the run types by comparing population means in these variables. To describe the gradient in these characteristics in relation to life histories, we looked for correlations among populations using Pearson's correlation coefficient (r). We compared age at smolting (freshwater age) to ocean age and total age to sex ratio (percentage of females).

RESULTS

In total, we analyzed data from 5,628 adult steelhead from spawning run years 2009–2010 through 2011–2012. Of those, 2,753 samples were from IPTD detections of adult fish trapped and PIT-tagged at Lower Granite Dam. An additional 2,729 samples were from adults collected at weirs, and 146 samples were collected by angling. Fork lengths ranged from 46 to 93 cm. Total age at spawning ranged from 3 to 8 years. Adults had smolted at ages from 1 to 5 years, and spent from 1 to 3 years in the ocean. All possible combinations of freshwater and ocean ages were found, except for smolting at 5 years and spending 3 years in the ocean before maturity. There were five categories of repeat spawners, most of which had first spawned after 1 year in the ocean. We found no evidence of fish on a third spawning run. The smallest sample sizes were from Lolo Creek (n = 65) and Secesh River (n = 76); the largest sample sizes were obtained from the Potlatch River (n = 858) and Imnaha River (n = 646).

The number of detections at BON of adults tagged as juveniles (n = 803) was smaller than the number sampled in the Snake River basin (see previous paragraph). Returning adults were detected at BON as early as June 1 and as late as November 6. The mean population sample size was 50 and ranged as low as 7 for Lolo Creek and Pahsimeroi River, and as high as 244 for Fish Creek.

Comparison to Current and Historic Fisheries Management Criteria

All populations had adults that were <78-cm FL (Figure 2). The median lengths of all putative B-run populations were quite close to the length criterion used to distinguish group-A and group-B populations, ranging from 74 cm (Big Creek) to 78 cm (Lolo Creek and South Fork Salmon River). In contrast, few A-run populations produced many adults ≥78-cm FL. The median length of A-run populations ranged from 59 cm (Pahsimeroi River) to 69 cm (Potlatch River). The median percentage of fish <78 cm in B-run populations was higher (52.7%) than the median percentage of fish ≥78 cm in A-run populations (0.9%; Table 1).

All populations had adults that passed BON after August 25, the date historically used to distinguish group-A and group-B steelhead (Table 1). However, the median passage date of all A-run populations was before August 25 and ranged from July 24 (Joseph Creek) to August 17 (Rapid River). All B-run populations, except Lolo Creek, had adults that arrived at BON before August 26. The median passage dates of B-run populations were after the medians of the A-run populations, ranging from August 19 (Big Creek) to September 11 (Lolo Creek). The median percentage of fish arriving before August 26 in B-run populations (17.6%) was higher than the median percentage of fish arriving after August 25 in A-run populations (12.4%).

There were varying percentages of classifications into the opposite fishery management group when the current and historic criteria for group A or group B in the Columbia River are

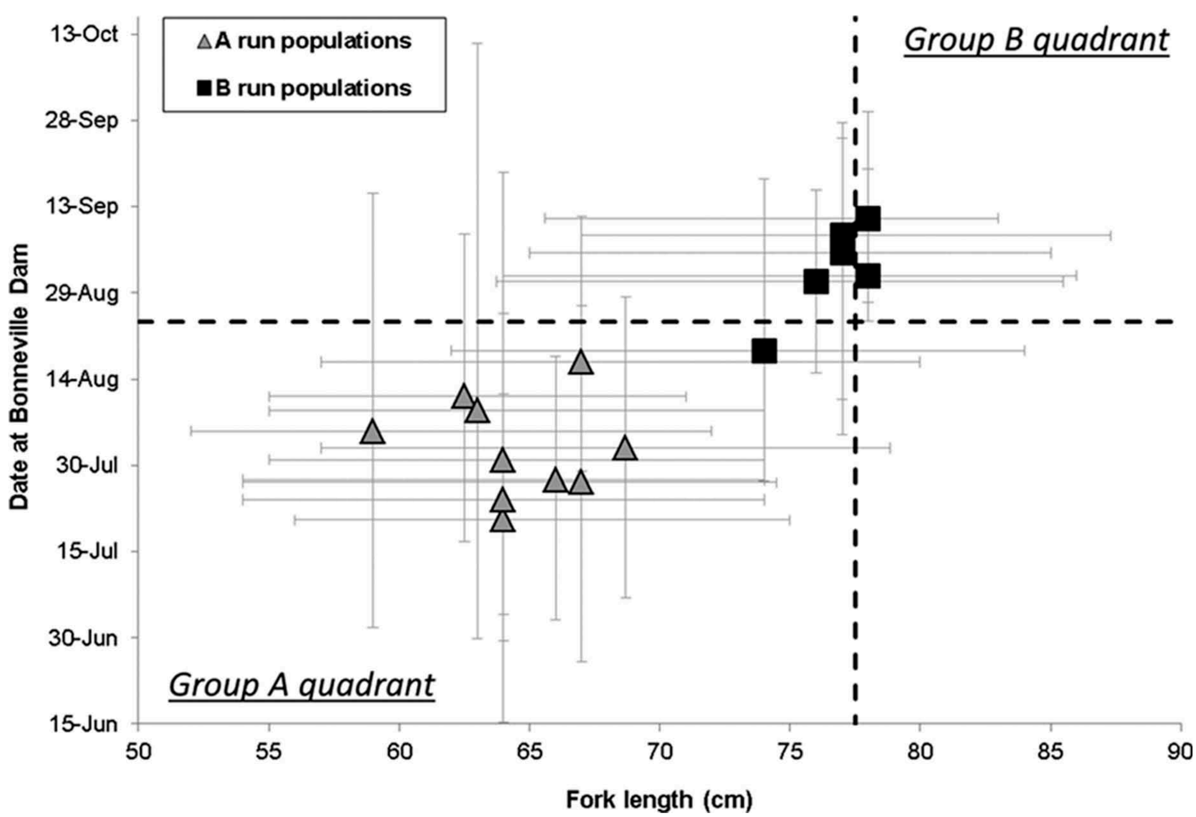

FIGURE 2. Population medians in length at spawning and return date at Bonneville Dam. The error bars are the 5% and 95% quantiles. The dashed lines represent the criteria separating group A and group B: length (78 cm) and date (August 25).

TABLE 1. Percentage of steelhead in each population that do not match the current length and historic run timing criteria used for fisheries management in the Columbia River for the putative run type assigned to that population. The current criterion is <78-cm FL for group A or ≥78 cm-FL for group B. The historic criterion was arrival at Bonneville Dam on or before August 25 for group A or after August 25 for group B. Populations are listed alphabetically within run type. Sample sizes are in parentheses.

Population	Length criterion (%)	Run timing criterion (%)
A-run populations		
Asotin Creek	2.6 (196)	9.1 (33)
Imnaha River	0.8 (646)	3.5 (144)
Joseph Creek	0.6 (359)	1.8 (56)
Lapwai Creek	1.0 (102)	15.0 (20)
Lemhi River	0.0 (116)	18.8 (32)
Pahsimeroi River	0.7 (670)	28.6 (7)
Potlatch River	8.3 (858)	11.4 (35)
Rapid River	9.6 (364)	42.5 (40)
Tucannon River	0.4 (236)	13.4 (67)
Upper Salmon River	1.4 (286)	7.1 (14)
B-run populations		
Big Creek	72.2 (263)	53.8 (26)
Fish Creek	55.1 (543)	18.5 (249)
Lolo Creek	46.2 (65)	0.0 (7)
Secesh River	63.2 (76)	16.7 (12)
South Fork Clearwater River	50.4 (115)	11.1 (9)
South Fork Salmon River	44.8 (500)	26.3 (57)

used to classify steelhead in the Snake River (Table 1). A steelhead from a B-run population was more likely to be identified as a group-A steelhead than a steelhead from an A-run population was to be identified as a group-B steelhead using the current (length-based) or historic (date-based) management criteria. The error bars in Figure 2 show the broad overlap among populations, but the central tendencies of each population were distributed along a trend leading from smaller, earlier arriving fish to larger, later-arriving fish.

Age Composition and Sex Ratio

Age structure among Snake River steelhead populations was quite variable (Figure 3). Of the 23 different combinations of freshwater ages, saltwater ages, and spawn checks, we found 19 in A-run populations and 17 in B-run populations. Few three-ocean fish or repeat spawners were observed in any population (<10% and <3%, respectively), but both occurred widely—in 12 of 16 populations and in 10 of 16 populations, respectively. Most populations were dominated by two-ocean fish, although the percentage varied. The mean percentage of two-ocean fish was 51.3% for A-run populations and 82.0% for B-run populations. Most Snake River steelhead smolted at 2 or 3 years. Again, the predominance of these two freshwater age-groups varied among populations. The mean percentage of fish that smolted at age 3 was 17.0% for A-run populations and 50.9% for B-run populations. Years spent in freshwater and the ocean were positively related (r = 0.67). Populations with more age-3 smolts tended to produce more two-ocean adults; therefore, the mean age at spawning was greater in populations that produce older smolts. Mean age at spawning ranged from 4.1 years (Pahsimeroi River) to 6.1 years (Secesh River). Mean age of A-run populations was 4.6 years, and mean age of B-run populations was 5.6 years.

The sex ratio was female biased in all populations (Figure 4) and ranged from 54.1% to 75.4% females. Older populations tended to have a greater percentage of females spawning (r = 0.84). There was a larger percentage of females in B-run populations (69.2%) than in A-run populations (60.8%).

DISCUSSION

The life history portfolio of wild Snake River steelhead is quite diverse; therefore, there was broad overlap among populations in several respects, forming a gradient in life history characteristics rather than a sharp dichotomous break. Most populations produced adults smaller and larger than 78 cm, and adults that returned to BON before and after August 26. The median lengths of all putative B-run populations were close to the length criterion that is used to classify group-B steelhead at BON; however, few A-run populations produced many adults ≥78 cm. The majority of fish in most populations had spent 2 years in the ocean, although the percentage was higher in B-run populations. The number of years spent in freshwater and salt water were positively correlated such that the mean age at spawning was greater in populations that produce older smolts. Sex ratio was female biased, and older populations tended to have a greater percentage of returning females. These results have implications for fisheries management in the Columbia River and conservation in the Snake River basin.

Implications for Fisheries Management

The abundance estimate of wild and hatchery group-A and group-B steelhead at BON is an important input into the Columbia River fisheries harvest management process mandated by the ongoing U.S. v. Oregon (1969) court case. Sport and nontribal commercial fisheries on salmonids (steelhead, Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*) may not exceed a 2% impact on either wild group-A or group-B steelhead (as estimated at BON). Tribal fisheries must remain under the specified steelhead harvest rate (13–20%, depending on spawning run size) on the total group-B passage count at BON. Group-B stocks have a run timing and length distribution more similar to fall-run Chinook Salmon than group-A stocks; therefore, they are more susceptible to harvest

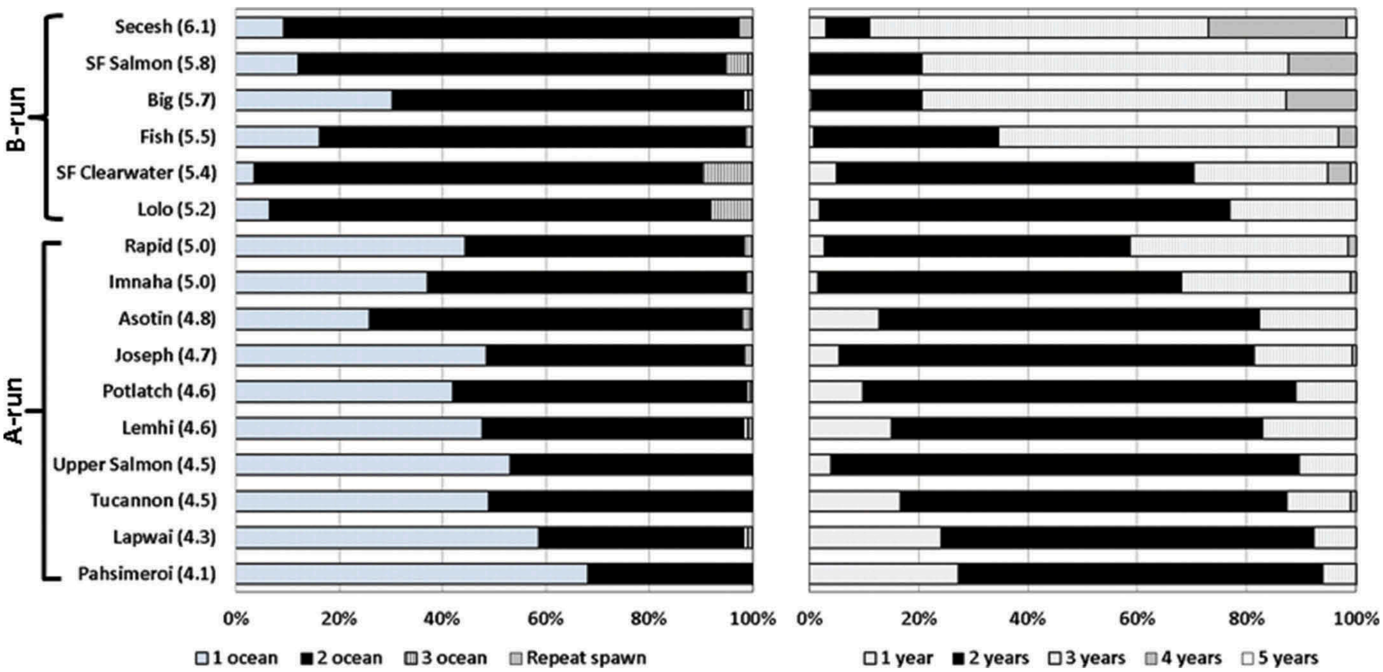

FIGURE 3. Age composition of selected Snake River steelhead populations. The left panel shows percentages by ocean age, including all repeat spawners combined. The right panel shows composition of smolt ages. Populations are arranged by mean total age at spawning (in parentheses), oldest at the top. Run type is indicated by brackets on the left.

in tribal fisheries, which are directed primarily at Chinook Salmon. Most upriver fall-run Chinook Salmon in the Columbia River are not listed under the ESA and are managed for harvest at rates from 21.5% to 45%. It is important that the assessment of the relevant steelhead groups be accurate to achieve salmon harvest objectives and to protect vulnerable wild steelhead populations. In actuality, these two objectives compete.

The current length-based steelhead classification system used in Columbia River fisheries was developed in the 1990s (ODFW and WDFW 2000). The suitability of the length criterion was developed by the IDFG based on hatchery fish. Its suitability for application to wild fish was assessed using length data collected during 1990–1992 from wild steelhead in the Salmon and Clearwater drainages (IDFG, unpublished data; Figure 5). It was concluded that the data were insufficient to make definitive statements about the percentage of larger and later-timed steelhead with regards to exact origin, but the length criterion could be used as an index of steelhead stock components in the fishery (ODFW and WDFW 2000). However, managers never thought all B-run populations were ≥78 cm, only that most steelhead ≥78 cm spawned in certain areas in Idaho. The length-based classification was intended to protect these less-abundant wild populations, as no other method to distinguish them was available at the time.

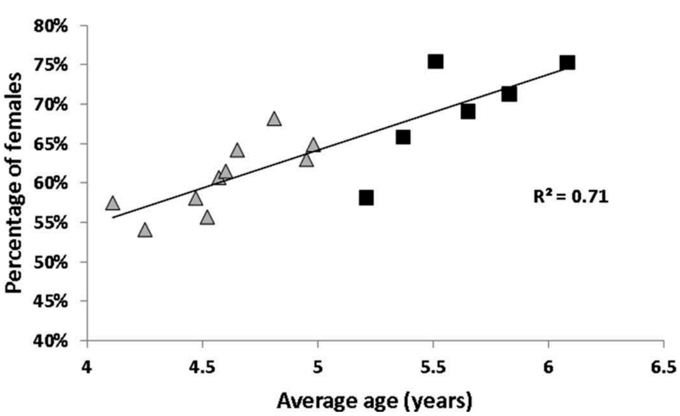

FIGURE 4. Relationship of mean age at spawn to proportion of females in Snake River steelhead populations. Triangles represent A-run populations and squares represent B-run populations.

We found proportionally fewer steelhead ≥78 cm in the six populations with 1990–1992 and current data, and that decline was greatest in two of the three B-run populations (Figure 5). Group-B fish were thought to spend typically 2 to 3 years in the ocean, but we found very few three-ocean steelhead. Although wild B-run populations may be more abundant than the group-B length index indicates, the proportion of fish ≥78 cm in these populations appears to have been reduced from when the length criterion was implemented.

Interestingly, when the Columbia River steelhead management scheme was revised in 1999, the steelhead arriving earlier at BON still tended to be smaller, while later steelhead tended to be larger

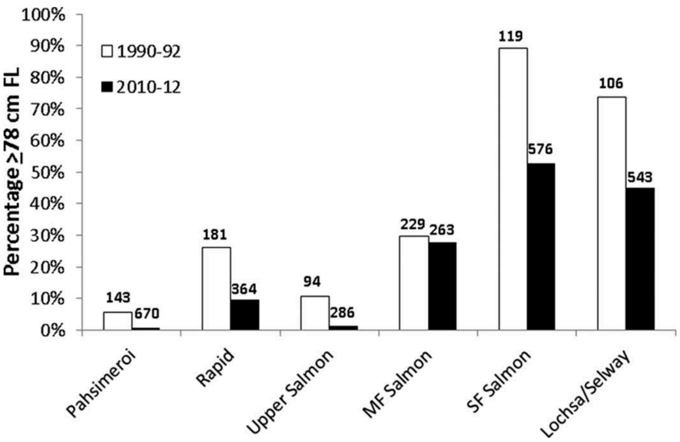

FIGURE 5. Comparison of percentage of steelhead ≥78 cm sampled in selected Idaho streams during 1990–1992 with comparable data in the present study. The Middle Fork Salmon River sample is compared with the present Big Creek sample, and the Lochsa–Selway rivers sample is compared with the present Fish Creek sample. Numbers above bars are the respective sample sizes.

(ODFW and WDFW 2000). The change in modal timing of migrations observed by Robards and Quinn (2002) may be driven largely by the increased abundance of hatchery steelhead derived mostly from A-run populations, coupled with a decreased abundance of wild B-run populations. We found that the order of arrival at BON was maintained by the wild populations examined in this study in terms of median arrival date. However, the population types cannot be distinguished upstream of BON by date because earlier arriving fish tend to migrate more slowly as they encounter warm water temperatures and mix with later arrivals (ODFW and WDFW 2000; High et al. 2006; Keefer et al. 2009). Therefore, the length criterion is more practical than the timing criterion for assessing fishery impacts upstream of BON but contains high error rates for B-run populations (>40% biased low). Genetic analysis of the steelhead harvest in the Columbia Rvier (e.g., Byrne et al. 2015) and samples collected at main-stem dams allows a much more specific estimation of impacts because the putative B-run populations can be identified with high accuracy in mixed-stock analyses using genetic data (Ackerman et al. 2014; Hess et al. 2016). Because all Snake River hatcheries genotype their broodstock (Steele et al. 2013), unclipped hatchery fish can be distinguished from wild fish so that impact rates on protected wild stocks can be accurately assessed.

Implications for Conservation

The two categories used for the management of steelhead in Columbia River fisheries were adopted for the conservation of wild Snake River populations in the absence of more specific data (ICTRT 2009). However, these broad categories mask the genetic and life history diversity that influences population dynamics and viability of wild steelhead populations. The A-run and B-run dichotomy is not supported by recent genetic studies (Nielsen et al. 2009; Blankenship et al. 2011; Ackerman et al. 2014; Matala et al. 2014). Genetic analyses suggest that B-run populations are polyphyletic; that is, B-run populations are more closely related to geographically proximate A-run populations than they are to distant B-run populations. Genetic structure in the Snake River basin is determined primarily by isolation by distance (e.g., Olsen et al. 2008; Ackerman et al. 2012b) and anthropogenic influences (e.g., out-of-basin transfers of hatchery fish), not by A-run and B-run lineages (Nielsen et al. 2009; Ackerman et al. 2012a). However, B-run populations are genetically distinct from their A-run neighbors and can be identified with a high level of confidence (Ackerman et al. 2014) such that more accurate population assessments can be done using genetic stock identification than those based on the current length criterion.

Evidence suggests that life history diversity makes salmonid populations more resilient and buffers them against extinction (Hilborn et al. 2003; Bisson et al. 2009; Greene et al. 2009; Schindler et al. 2010), particularly in stocks where abundance is low due to natural or anthropogenic influences (Courter et al. 2013). Steelhead life histories are more correlated by year of ocean entrance than by brood year (Moore et al. 2014); therefore, variation in freshwater age can buffer against ocean variability. Furthermore, repeat spawners may stabilize population dynamics by producing more offspring over their lifetime than maiden spawners (Seamons and Quinn 2010) as well as increasing the distribution of ages in the spawning population (Moore et al. 2014). Greater diversity in total ages of returning adults helps maintain genetic diversity in populations by increasing overlap among generations.

Life history expression in anadromous salmonids is strongly influenced by freshwater growth (Sloat et al. 2014). Fish tend to mature later and at larger sizes when growth rate is reduced by low temperatures (Berrigan and Charnov 1994). The B-run steelhead populations occur in the higher-elevation terminal drainages of the Snake River (e.g., Lochsa River, Selway River, South Fork Clearwater River, Middle Fork Salmon River, and South Fork Salmon River; Figure 1). Brannon et al. (2004) hypothesized that local environmental conditions in these drainages produce a steelhead phenotype that is older at juvenile emigration, larger at maturity, and returning later from salt water, consistent with the data we present. However, consistent selection against older, larger-bodied fish will reduce the fitness of delayed maturation (Fujiwara 2008). Older age at maturity is negatively correlated to intrinsic population growth rate (Hutchings et al. 2012). If managers desire to conserve the distinctive characteristics of wild steelhead populations in the Snake River basin, then the factors that produce them must be understood as well as their ties to fitness. Because steelhead populations are so diverse, arbitrary classifications will be wrong to a greater or lesser extent; therefore, genetic stock identification and population-specific sampling will be more useful than the current categories, in which fisheries management and conservation objectives are easily confused.

In conclusion, we found that there is a continuum of life history diversity in wild Snake River steelhead populations, which makes simple categorization fraught with error (Table 1). Although the run-type dichotomy was the best means available for the management of Columbia River fisheries in the past, it is not useful for monitoring population status, assessing ESA recovery plans, and tracking progress toward delisting from the ESA. There are new tools and methods (parentage-based tagging, genetic stock identification, and IPTDs; Campbell et al. 2012; Steele et al. 2013; Hess et al. 2016; this study) that give finer resolution of population abundance and diversity. The utility of genetic techniques for monitoring catch composition in mixed-stock fisheries is well documented (Shaklee et al. 1999). Recent developments in applications of genetic technology have greatly increased our understanding of salmonid stock behavior, distribution, and contributions to fisheries (e.g., Satterthwaite et al. 2014; Bellinger et al. 2015; Bradbury et al. 2016). These tools provide a unifying framework for the assessment of fisheries management and conservation objectives. A combination of genetic stock identification at main-stem dams and population-specific monitoring in natal streams (such as presented here) will allow estimation of abundance and productivity metrics at a scale necessary for assessments of population viability and extinction risk.

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REFERENCES

Ackerman, M. W., J. McCane, C. A. Steele, M. R. Campbell, A. P. Matala, J. E. Hess, and S. R. Narum. 2012a. Chinook and steelhead genotyping for genetic stock identification at lower granite dam. Annual Report to the Bonneville Power Administration, Project 2010-026, Portland, Oregon.

Ackerman, M. W., W. D. Templin, J. E. Seeb, and L. W. Seeb. 2012b. Landscape heterogeneity and local adaptation define the spatial genetic structure of Pacific salmon in a pristine environment. Conservation Genetics 14:483–498.

Ackerman, M. W., N. Vu, J. McCane, C. A. Steele, M. R. Campbell, A. P. Matala, J. E. Hess, and S. R. Narum. 2014. Chinook and steelhead genotyping for genetic stock identification at lower granite dam. Annual Report to the Bonneville Power Administration, Project 2010-026-00, Portland, Oregon.

Bellinger, M. R., M. A. Banks, S. J. Bates, E. D. Crandall, J. C. Garza, G. Sylvia, and P. W. Lawson. 2015. Geo-referenced, abundance calibrated ocean distribution of Chinook Salmon (*Oncorhynchus tshawytscha*) stocks across the West Coast of North America. PLOS (Public Library of Science) ONE [online serial] 10(7):e0131276.

Berrigan, D., and E. L. Charnov. 1994. Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. Oikos 70:474–478.

Bisson, P. A., J. B. Dunham, and G. H. Reeves. 2009. Freshwater ecosystems and resilience of Pacific salmon: habitat management based on natural variability. Ecology and Society [online serial] 14(1):45.

Blankenship, S. M., M. R. Campbell, J. E. Hess, M. A. Hess, T. W. Kassler, C. C. Kozfkay, A. P. Matala, S. R. Narum, M. M. Paquin, M. P. Small, J. J. Stephenson, K. I. Warheit, and P. Moran. 2011. Major lineages and metapopulations in Columbia River *Oncorhynchus mykiss* are structured by dynamic landscape features and environments. Transactions of the American Fisheries Society 140:665–684.

Bradbury, I. R., L. C. Hamilton, G. Chaput, M. J. Robertson, H. Goraguer, A. Walsh, V. Morris, D. Reddin, J. B. Dempson, T. F. Sheehan, T. King, and L. Bernatchez. 2016. Genetic mixed stock analysis of an interceptor Atlantic Salmon fishery in the Northwest Atlantic. Fisheries Research 174:234–244.

Brannon, E. L., M. S. Powell, T. P. Quinn, and A. Talbot. 2004. Population structure of Columbia River basin Chinook Salmon and steelhead trout. Reviews in Fisheries Science 12:99–232.

Braun, D. C., J. W. Moore, J. Candy, and R. E. Bailey. 2016. Population diversity in salmon: Linkages among response, genetic and life history diversity. Ecography 39:317–328.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Wauneta, and I. V. Lagomarsino. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-27.

Byrne, A., J. Hymer, S. Ellis, R. Dick, K. Keller, C. A. Steele, M. E. Hess, M. Begay, and T. Miller. 2015. A genetic analysis of the summer steelhead stock composition in the Columbia River and Snake River tribal and sport fisheries. Idaho Department of Fish and Game, Report 15-06, Boise.

Campbell, M. R., C. C. Kozfkay, T. Copeland, W. C. Schrader, M. W. Ackerman, and S. R. Narum. 2012. Estimating abundance and life history characteristics of threatened wild Snake River steelhead stocks by using genetic stock identification. Transactions of the American Fisheries Society 141:1310–1327.

Courter, I. I., D. B. Child, J. A. Hobbs, T. M. Garrison, J. J. G. Glessner, and S. Duery. 2013. Resident rainbow trout produce anadromous offspring in a large interior watershed. Canadian Journal of Fisheries and Aquatic Sciences 70:701–710.

Ford, M. J., A. Albaugh, K. Barnas, T. Cooney, J. Cowen, J. Hard, R. Kope, M. McClure, P. McElhany, J. Myers, N. Sands, D. Teel, and L. Weitkamp. 2011. Status review update for Pacific salmon and steelhead listed under the Endangered Species Act: northwest. NOAA Technical Memorandum NOAA-TM-NWFSC-113.

Fryer, J. K., J. Whiteaker, and D. Kelsey. 2012. Upstream migration timing of Columbia basin Chinook Salmon, Sockeye Salmon, and steelhead in 2010. Columbia River Inter-Tribal Fish Commission, Technical Report 12-02, Portland, Oregon.

Fujiwara, M. 2008. Effects of an autocorrelated stochastic environment and fisheries on the age at maturity of Chinook Salmon. Theoretical Ecology 1:89–101.

Greene, C. M., J. E. Hall, K. R. Guilbault, and T. P. Quinn. 2009. Improved viability of populations with diverse life-history portfolios. Biology Letters 6:382–386.

Hendry, A. P., T. Bohlin, B. Jonsson, and O. K. Berg. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. Pages 92–125 *in* A. P. Hendry and S. C. Stearns, editors. Evolution illuminated: salmon and their relatives. Oxford University Press, New York.

Hess, J. E., M. W. Ackerman, J. K. Fryer, D. J. Hasselman, C. A. Steele, J. J. Stephenson, J. M. Whiteaker, and S. R. Narum. 2016. Differential adult migration-timing and stock-specific abundance of steelhead in mixed stock assemblages. ICES Journal of Marine Science 73:2606–2615.

High, B., C. A. Peery, and D. H. Bennett. 2006. Temporary staging of Columbia River summer steelhead in coolwater areas and its effect on migration rates. Transactions of the American Fisheries Society 135:519–528.

Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences of the USA 100:6564–6568.

Hutchings, J. A., R. A. Myers, V. B. Garcia, L. O. Lucifora, and A. Kuparinen. 2012. Life-history correlates of extinction risk and recovery potential. Ecological Applications 22:1061–1067.

ICTRT (Interior Columbia Technical Recovery Team). 2009. Current status reviews: interior Columbia basin salmon ESUs and steelhead DPSs, volume 1: Snake River basin ESUs/DPSs. National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Seattle.

Keefer, M. L., C. A. Peery, and B. High. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations. Canadian Journal of Fisheries and Aquatic Sciences 66:1734–1747.

Kendall, N. W., J. R. McMillan, M. R. Sloat, T. W. Buehrens, T. P. Quinn, G. R. Pess, K. V. Kuzishchin, M. M. McClure, and R. W. Zabel. 2015. Anadromy and residency in steelhead and Rainbow Trout (*Oncorhynchus mykiss*): a review of patterns and processes. Canadian Journal of Fisheries and Aquatic Sciences 72:319–342.

Mallett, J. L. 1974. Inventory of salmon and steelhead resources, habitat, use and demands. F-58-R-1, Boise.

Matala, A. P., M. W. Ackerman, M. R. Campbell, and S. R. Narum. 2014. Relative contributions of neutral and non-neutral genetic differentiation to inform conservation of steelhead trout across highly variable landscapes. Evolutionary Applications 7:682–701.

McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonids populations and the recovery of evolutionarily significant units. NOAA Technical Memorandum NMFS-NWFSC-42.

Moore, J. W., J. D. Yeakel, D. Peard, J. Lough, and M. Beere. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. Journal of Animal Ecology 83:1035–1046.

Nielsen, J. L., A. Byrne, S. L. Graziano, and C. C. Kozfkay. 2009. Steelhead genetic diversity at multiple spatial scales in a managed basin: Snake River, Idaho. North American Journal of Fisheries Management 29:680–701.

NMFS (National Marine Fisheries Service). 1997. Endangered and threatened species: listing of several evolutionarily significant units (ESUs) of West Coast steelhead. Federal Register 62:159(18 August 1997):43937–43954.

ODFW (Oregon Department of Fish and Wildlife) and WDFW (Washington Department of Fish and Wildlife). 2000. Joint staff report concerning the 2000 in-river commercial harvest of Columbia River fall Chinook Salmon, summer steelhead, Coho Salmon, and sturgeon. Available: http://wdfw.wa.gov/fishing/crc/staff_reports.html. (January 2017).

Olsen, J. B., B. G. Flannery, T. D. Beacham, J. F. Bromaghin, P. A. Crane, C. F. Lean, K. M. Dunmall, and J. K. Wenburg. 2008. The influence of hydrographic structure and seasonal run timing on genetic diversity and isolation-by-distance in Chum Salmon (*Oncorhynchus keta*). Canadian Journal of Fisheries and Aquatic Sciences 65:2026–2042.

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

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle.

Robards, M. D., and T. P. Quinn. 2002. The migratory timing of adult summer-run steelhead in the Columbia River over six decades of environmental change. Transactions of the American Fisheries Society 131:523–536.

Satterthwaite, W. H., M. S. Mohr, M. R. O'Farrell, E. C. Anderson, M. A. Banks, S. J. Bates, R. Bellinger, L. A. Borgeson, E. D. Crandall, J. C. Garza, B. J. Kormos, P. W. Lawson, and M. L. Palmer-Zwahlen. 2014. Use of genetic stock identification data for comparison of the ocean spatial distribution, size at age, and fishery exposure of an untagged stock and its indicator: California coastal versus Klamath River Chinook Salmon. Transactions of the American Fisheries Society 143:117–133.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–612.

Seamons, T. R., and T. P. Quinn. 2010. Sex-specific patterns of lifetime reproductive success in single and repeat breeding steelhead trout (*Oncorhynchus mykiss*). Behavioral Ecology and Sociobiology 64:505–513.

Shaklee, J. B., T. D. Beacham, L. Seeb, and B. A. White. 1999. Managing fisheries using genetic data: case studies from four species of Pacific Salmon. Fisheries Research 43:45–78.

Sloat, M. R., D. J. Fraser, J. B. Dunham, J. A. Falke, C. E. Jordan, J. R. McMillan, and H. A. Ohms. 2014. Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines. Reviews in Fish Biology and Fisheries 24:689–707.

Steele, C. A., E. C. Anderson, M. W. Ackerman, M. A. Hess, N. R. Campbell, S. R. Narum, and M. R. Campbell. 2013. A validation of parentage-based tagging using hatchery steelhead in the Snake River basin. Canadian Journal of Fisheries and Aquatic Sciences 70:1046–1054.

Thorpe, J. E., M. Mangel, N. B. Metcalfe, and F. A. Huntingford. 1998. Modelling the proximatae basis of salmonid life-history variation, with application to Atlantic Salmon *Salmo salar* L. Evolutionary Ecology 12:581–599.

U.S. v. Oregon. 1969. 302 F. Supp. 899 (Dist. of Oregon).

WDFW (Washington Department of Fish and Wildlife) and ODFW (Oregon Department of Fish and Wildlife). 2002. Columbia River fish runs and fisheries 1938–2000. Available: http://wdfw.wa.gov/fishing/crc/staff_reports.html. (January 2017).

Wright, K. K., W. Schrader, L. Reinhardt, K. Hernandez, C. Hohman, and T. Copeland. 2015. Process and methods for assigning ages to anadromous salmonids from scale samples. Idaho Department of Fish and Game, Report 15-03, Boise.