Use of Parentage Assignment and DNA Genotyping to Validate Scale Analysis for Estimating Steelhead Age and Spawning History

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Abstract.—Sound fisheries management depends on understanding life history characteristics, such as age at maturity, migration, and spawning history; hard parts, such as scales and otoliths, are commonly used to estimate values for these traits. Validation of these techniques is often difficult but critical because errors in mean values for a population can result in erroneous estimates of sustainable exploitation rates. In this study, we compared information on age and spawning history derived from genetic analysis with information from scale analysis for 1,836 individual steelhead Oncorhynchus mykiss representing two life history stages (smolt and mature adult); these fish were of hatchery and wild origin and were sampled from two rivers in Washington State over a period of 19 years. Aging error rates were less than 5% for both wild smolts and hatchery adults, but the error rate for wild adults was much higher (13%; 95% confidence interval [CI] = 1.82–29.22%). Adult scale ages were biased; scale readers typically overestimated the ages of younger fish and underestimated the ages of older fish. In addition to the errors in age estimation, repeat spawners were misclassified as virgin spawners 6.5% of the time (95% CI = 0.79–20.26%). The higher error rates obtained in using scales for aging and identifying repeat spawning in wild adults may partly stem from the more complex life history relative to that of smolts or hatchery-origin adults; these results highlight the need for verification of scale analysis, especially for wild steelhead populations.

Fish life history traits, such as age, migration, and spawning history, are fundamental to understanding the basic ecology of fishes and also serve as the foundation for sound fishery management. Errors in estimating the age distribution of a population, the age at first reproduction, and the frequency of reproduction could result in inappropriate exploitation rates. Many hard parts are used to estimate age and reproductive history of individuals, but scales are commonly selected to infer life history because material is consistently added to the scales as fish grow and because scales can be removed without sacrificing the fish (unlike, for example, otoliths or opicular bones; DeVries and Frie 1996; Campana 2001; Riffliart et al. 2006). Indeed, scales have been used to characterize the life history of fishes since the 17th century (Jackson 2007) and have been used in studies of semelparous and iteroparous anadromous salmonids for nearly a century (Gilbert 1913; Went 1964; Withler 1966; Gardner 1976).

Ages of freshwater or anadromous fishes in temperate climates are estimated by counting ridges that are deposited in regular patterns coinciding with the fish’s growth (Das 1994). Growth is typically fast during the summer, resulting in circuli that are spaced farther apart, whereas growth during the winter is slower, resulting in circuli that are spaced closely; an annulus is therefore produced, and the number of annuli is interpreted as age in years (Das 1994).

The scales of anadromous fishes have two patterns of growth corresponding to (1) the period spent in freshwater, when closely spaced annuli are produced, and (2) the saltwater growth period, which is characterized by annuli that are spaced farther apart because the fish grow more rapidly (Koo 1962; Davis and Light 1985). Iteroparous anadromous fishes, such as steelhead Oncorhynchus mykiss and Atlantic salmon Salmo salar, migrate back to the sea after spawning and (if they survive) return to freshwater to spawn again one or more years later. Sexual maturation and

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1 Retired.
the associated anorexia exhibited during and after the migration back to freshwater generate what are called spawn marks or spawn checks, which are irregular regions of resorption of saltwater circuli at the margin of the scale (Davis and Light 1985; Persson et al. 1995). These irregularities are preserved in the scale; the resumption of growth at sea leads to the deposition of more conventional circuli at the margin of the scale, leaving the spawn check visible between regions of normal circuli.

Using scales for interpreting life history can be problematic (Davis and Light 1985). Damaged scales may have scars or marks that obscure accurate life history determination upon examination. Scales are often lost during a fish’s initial migration from freshwater to salt water. Lost scales are regenerated by the fish; however, all record of growth prior to loss of the original scale is absent from the regenerated scale (Davis and Light 1985). If the fish experiences a constant growth rate, clear distinctions between periods of seasonal growth may be absent, making accurate aging difficult. Additional problems exist for reading the scales of iteroparous fishes. Bands of resorbed scale may occur in sick or starving fish (Persson et al. 1995), and this might cause scale readers to infer a spawning migration that did not occur. Resorption during the second spawning migration may also obliterate not only any growth that may have occurred but also the spawn check of the first migration. In this case, a scale reader might count fewer spawning migrations than actually occurred.

It is important to quantify the occurrence of these types of errors in scale age assignments by using known-age fish; indeed, Beamish and McFarlane (1983) characterized validation as the “forgotten requirement” in age and life history research. Accuracy can be assessed by combining scale reading with marking or tagging techniques (Beamish and McFarlane 1983; DeVries and Frie 1996). Modern molecular tools of DNA fingerprinting and parentage analysis provide alternative approaches for validation of scale readings in age and spawning history determination, and our goal was to apply these approaches to the life history of steelhead. Several classes of errors are possible when reading steelhead scales because steelhead vary in the number of years spent in freshwater prior to seaward migration and in the number of years spent at sea prior to the first spawning migration. They are also iteroparous, so there may be one spawning migration or multiple spawning migrations that might or might not occur in consecutive years (Withler 1966; Burgner et al. 1992; Busby et al. 1996). Very few studies have evaluated the accuracy of scale aging for steelhead, and these few have focused on young, nonanadromous fish (Maceina et al. 2007). To characterize the accuracy of scale analysis for steelhead, we first used DNA-based parentage analysis to verify ages inferred from patterns of scale annulus spacing. We then validated inferences about fish spawning history drawn from examination of scales.

Methods

Sampling sites and methods.—Adult winter-run (ocean-maturing) steelhead were intercepted during their upstream spawning migration in two Washington State streams: Snow Creek in Jefferson County and Forks Creek in Pacific County. Details on the sampling at these streams have been provided elsewhere (Mackey et al. 2001; Seamons et al. 2004). Briefly, both streams have permanent weirs operated by the Washington Department of Fish and Wildlife (WDFW) to trap fish (at Snow Creek) or divert them into holding areas (associated with the Forks Creek Hatchery, operated by WDFW). The fish captured in Snow Creek were all of wild origin. Fish were lightly anesthetized (buffered tricaine methanesulfonate) for sampling, and a small hole was punched in one operculum; fish were released alive either upstream or downstream of the weir to continue their migration. At Forks Creek, hatchery-produced adults, which were identifiable by a clipped adipose fin, were killed at the hatchery. Adults with intact adipose fins (indicating that they had been naturally spawned) were released alive either upstream or downstream of the weir.

All adults were measured for fork length, and sex was determined based on external characteristics. Scales were removed from the recommended region (posterior to the dorsal fin and approximately four scale rows above the lateral line; Davis and Light 1985) and were mounted on cards for later examination. Tissue was removed from the upper lobe of the caudal fin, preserved, and stored in 95% ethanol. All steelhead smolts were captured at the Snow Creek weir as they migrated downstream to the ocean. Approximately 20% of the smolts were anesthetized, measured for fork length, and sampled for scales and fin clips as described above for adults.

Our methods of processing tissue and DNA samples have been described in detail elsewhere (Seamons et al. 2004; Hauser et al. 2006) and are only briefly summarized here. Extraction of DNA from scales or fin clips was performed by using Qiagen DNeasy 96-well tissue DNA extraction kits (Qiagen, Inc., Valencia, California) according to the manufacturer’s guidelines. Polymerase chain reaction (PCR) was used to amplify alleles at 8 (Forks Creek) or 12 (Snow Creek) microsatellite loci, and alleles were visualized and size fractionated on a MegaBACE 1000 capillary
DNA sequencer. To find systematic problems with the genetic data, we tested for deviations from expected Hardy–Weinberg equilibrium (HWE) proportions with a two-tailed test using the Markov chain method implemented in GENEPOP version 3.4 (Raymond and Rousset 1995). The significance of the probability values was adjusted using the sequential Bonferroni approach of Rice (1989). Observed and expected values of heterozygosity and the inbreeding coefficient \( F_{IS} \) were also calculated using GENEPOP.

Scales were prepared by following the protocols defined by Bernard and Myers (1996). At least six scales from each Snow Creek steelhead (smolt or adult) were mounted on gum cards. One or more scales from each Forks Creek adult steelhead were mounted on gum cards. When only one scale was mounted, it was either the only scale available or the best of the available scales (e.g., had no scale damage and little or no regeneration) based on examination using a dissecting microscope. Acetate impressions of scales were read using a microfiche reader fitted with a 15-mm lens. Length, origin (hatchery or wild), and sex were known to the reader during scale examination. Scales from Snow Creek adults and smolts were read by one of the authors; scales from Forks Creek fish were read by another author.

Estimation of scale reading errors.—Validation of an aging technique requires known-age individuals. Known ages are typically obtained by physically tagging the fish. In our systems, known ages were determined from the inferred parent–offspring relationship and the years in which parents and offspring spawned or were sampled. There is some error associated with inferring parent–offspring relationships, and this error depends partly on how the relationships are determined. To create a gold standard of known ages, we used exclusion to determine our parent–offspring relationships; in other words, we did not allow for any genetic mismatches between parents and offspring when we determined these relationships. Any genotyping or processing error that occurred was much more likely to exclude a true parent than to include a false parent.

All adults that were captured and sampled were used as potential parents. For Snow Creek, this included putative stray hatchery fish (identified by a missing adipose fin) and coastal cutthroat trout \( O. clarkii clarkii \). Parents were assigned to individual smolt and adult offspring by use of the principles of exclusion. That is, only adults that shared at least one allele at each locus with the putative offspring were called the true parents, and they had to match the opposite allele at each locus. Our power to exclude was high; global exclusion probabilities for first and second parents (as calculated using Cervus version 3.0; Kalinowski et al. 2007) were 0.99999969 and 0.999999994, respectively, for the 12 loci screened in Snow Creek steelhead and 0.99985561 and 0.99999742, respectively, for the eight loci screened in Forks Creek steelhead. In some cases, all adults except one were genetically excluded as parents, and we concluded that one but not both parents had been sampled. Although the chance of matching a single parent is higher than the probability of matching two parents simultaneously (Marshall et al. 1998), in our data sets the probability of a random match of a single parent was less than 1 in 1,000 for Snow Creek steelhead (Seamons et al. 2007) and less than 1 in 100 for Forks Creek steelhead.

Aging errors could occur in the freshwater zone, the saltwater zone, or both zones, but our approach only allowed us to identify errors in total age for the adults. Total ages were determined by subtracting the year in which the parents spawned from the year in which offspring were sampled as smolts or adults. Offspring with parentage-based ages that were ambiguous (i.e., because repeat spawning was identified for both assigned parents or the single assigned parent) were omitted from analysis. Aging error rates were calculated as the percentage of individuals for which age estimates were not in agreement between parentage and scale methods; 95% confidence intervals (CIs) were calculated for each error rate (confidence limits for population proportions; Zar 1999). We also investigated bias and precision in aging methods by plotting age bias and calculating the coefficient of variation (Campana et al. 1995). Given that individual lengths were available to scale readers at the time of age estimation, we suspected that any bias we found might be related to length. We performed one-factor analysis of variance (ANOVA) on the lengths of groups defined by their match–mismatch category (1-year underestimation by scale reading, matched ages, or 1-year overestimation by scale reading). To identify differences between categories, we performed Tamhane’s post hoc test because it assumes unequal variances. All statistical tests were performed in the Statistical Package for the Social Sciences version 12.0 (SPSS, Inc., Chicago, Illinois).

Repeat spawners were identified by the presence of a spawning check on their scales (Davis and Light 1985; Persson et al. 1995). Errors in determining the spawning history by scale reading were estimated by comparing individuals that were genetically identified as repeat spawners (based on the presence of identical individual genotypes in consecutive brood years) with the scale-determined spawning history from the second year of sampling. As with aging validation, validation of spawning history depends on little or no error being
present in one of the two methods being compared. As a measure of confidence in the genetic identification of repeat spawners, we calculated the probability of identity \( P_{\text{ID}} \), an estimate of the probability of drawing two identical genotypes from the population at random (Taberlet and Luikart 1999); the \( P_{\text{ID}} \) was determined for all loci with brood years pooled. A very small \( P_{\text{ID}} \) indicated a very small chance that two samples with identical genotypes were from different individuals. We also calculated an unbiased \( P_{\text{ID}} \) estimate \( P_{\text{ID, unbiased}} \) and an estimate of the probability that siblings have identical genotypes \( P_{\text{ID, same}} \), which also serves as an upper bound to the distribution of theoretical \( P_{\text{ID}} \) values (Taberlet and Luikart 1999).

### Results and Discussion

#### Genetic Data and Parentage

No serious systematic problems were found in the genetic data. Among tests of deviation from HWE, only 6 of 240 tests for Snow Creek and only 4 of 112 tests for Forks Creek were statistically significant after corrections for multiple comparisons (Hauser et al. 2006; Seamons et al. 2007). These deviations were found in loci that were believed to have low-frequency null alleles and did not preclude successful assignment of parents. At least one parent was assigned to 84% of Snow Creek smolts. Of the smolts for which parentage could be fully or partially assigned, 50% were assigned two parents, 48% were only assigned a mother, and 2% were only assigned a father (Seamons 2005). We assigned at least one parent to 66% of Snow Creek adults. Of the adults with parentage assignments, 37% were assigned both parents, 53% had only a mother assigned, and 10% had only a father assigned (Seamons et al. 2007). Of the Forks Creek adult steelhead examined for parentage, 75% were assigned at least one parent. Of those adults, 93% were assigned two parents, 3.5% were assigned a mother only, and 3.5% were assigned a father only.

#### Aging Error Rate

Sixty-three percent (1,088 of 1,717) of smolts captured in Snow Creek between 1999 and 2003 were aged using both scales and parentage analysis (Table 1). The unused portion consisted of fish (1) whose scales were not sampled (417 individuals), (2) to which parents could not be assigned (192 individuals), and (3) whose only inferred parent was a repeat spawner, so age could not be determined from parentage data (20 individuals). Ages estimated by scale analysis ranged from 1 to 4 years (average = 2.06 years, SD = 0.43), and ages determined by parentage ranged from 1 to 3 years (average = 2.05 years, SD = 0.42). Smolt ages based on scale examination were precise and showed little evidence of bias (Figure 1a). However, parentage and scale ages were different in 42 individuals (error rate = 3.86%; 95% CI = 0.48–9.69%); all differences were by just 1 year. Ages were more often overestimated by scale analysis (31 occurrences) than underestimated (11 occurrences; chi-square test statistic \( \chi^2 = 9.52, df = 1, \alpha = 0.05, P = 0.002 \)). The average length of fish with underestimated ages (154 mm) was similar to the average length of fish with corroborated ages (158 mm), whereas fish with overestimated ages were much larger than the other two groups (average = 224 mm; one-factor ANOVA: \( F = 77.87, df = 2, 1,086, \alpha = 0.05, P < 0.001 \); Tamhane’s post hoc test: \( P < 0.001 \)). Perhaps the appearance of a scale from a fish that grew rapidly or some bias associated with reader knowledge of fish size resulted in these overestimations.

In Snow Creek, 1,073 adult fish were sampled between 1982 and 2004. Of those, 387 (36%) were aged using both scales and parentage analysis (Table 1). The remainder of the sample included 281 fish whose parents were unidentified, 269 fish whose parents returned before 1982 and therefore were not sampled, 121 fish with regenerated scales, 10 fish whose scales were not sampled, and 5 fish with scales that were considered unreadable. Total age estimated by scales and parentage ranged from 2 to 6 years (scales: average = 4.05 years, SD = 0.50; parentage: average = 4.02 years, SD = 0.56). Overall, there appeared to be a tendency to overestimate the age of fish younger than age 4 and to underestimate the age of fish older than age 4, and adult ages were less precise than ages from smolt scales (Figure 1b). The ages

### Table 1.—Number (n) of steelhead sampled from Snow and Forks creeks, Washington; number for which age was estimated from scales, genetically determined parentage, or both methods (numbers of hatchery [H] and wild [W] fish are given in parentheses); number and rate of errors in scale-based age relative to parentage-based age; and number of scale-based errors that involved age overestimation or underestimation.

<table>
<thead>
<tr>
<th>Location</th>
<th>Stage</th>
<th>Total n</th>
<th>Scales n</th>
<th>Parentage n</th>
<th>Scales and parentage n (H/W)</th>
<th>Error n</th>
<th>Error rate (%)</th>
<th>Overestimated</th>
<th>Underestimated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snow Creek</td>
<td>Smolts</td>
<td>1,717</td>
<td>1,300</td>
<td>1,440</td>
<td>1,088 (0/1,088)</td>
<td>42</td>
<td>3.86</td>
<td>53</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>1,073</td>
<td>841</td>
<td>517</td>
<td>387 (0/387)</td>
<td>52</td>
<td>13.44</td>
<td>30</td>
<td>22</td>
</tr>
<tr>
<td>Forks Creek</td>
<td>Adults</td>
<td>2,525</td>
<td>779</td>
<td>1,613</td>
<td>361 (352/9)</td>
<td>9</td>
<td>2.50</td>
<td>4</td>
<td>5</td>
</tr>
</tbody>
</table>
determined by the two methods differed in 52 individuals (error rate = 13.44%; 95% CI = 1.82–29.22%); for 50 of these fish, the difference was only 1 year. Age determined from scales was lower than the true age in 22 cases and higher than the true age in 30 cases. The length of fish whose ages were overestimated by scale analysis (average = 577 mm) tended to be smaller than the lengths of fish with underestimated ages (644 mm) or corroborated ages (628 mm; one-factor ANOVA: F = 10.05, df = 2, 382, α = 0.05, P < 0.001; Tamhane’s post hoc test: P = 0.063). Generally, three types of fish were misclassified. First, small fish that had apparently not been to sea were often classified incorrectly. Ten of the 30 fish with overestimated ages based on scales and 5 of the 22 fish with underestimated ages had apparently not been to sea. Such fish had all their growth and annuli in the freshwater region of the scale, which is more difficult to read than the marine region, and this difficulty may have contributed to the errors. Second, some large age-4 fish were classified as age 5. This is understandable based on the large size of the scale and some possible bias caused by reader knowledge of fish size. Finally, three fish with ages that were underestimated by scale analysis were repeat spawners. The resorption of scale material during a spawning migration may have obliterated one annulus from the marine region of the scale, causing the misclassification. No other obvious patterns of misclassification were apparent.

In Forks Creek, 2,525 hatchery-produced and wild adult steelhead were sampled between 1996 and 2003. Of those, 361 fish (352 hatchery and 9 wild fish) had both scale age and parentage data (Table 1). The adults that could not be used for analysis included 770 fish whose parents returned before 1996 and thus were not sampled, 454 fish whose scales were not read, 495 fish with regenerated scales, 22 fish with unreadable scales, 181 fish to which parents were not assigned, 5 fish with PCR amplification problems, and 237 fish whose parentage-based age was known to the scale reader at the time of scale examination. Total ages inferred from scales and parentage analysis ranged from 3 to 5 years (scales: average = 3.16 years, SD = 0.39; parentage: average = 3.16 years, SD = 0.41). The ages of older fish were consistently underestimated, but no pattern of bias was apparent in the estimated age of younger fish (Figure 1c). Parentage- and scale-inferred ages were different in nine individuals (error rate = 2.5%; 95% CI = 0.30–6.90%), and estimates differed by just 1 year for all but one of these fish. Differences in age were split nearly equally between overestimation by scales (4 of 9 fish) and underestimation by scales (5 of 9 fish). Fewer errors were found in the Forks Creek scale analysis than in the Snow Creek scale analysis; this

![Figure 1](image_url)

FIGURE 1.—Age bias plots illustrating pairwise comparisons of scale-based age with age estimated from genetically determined parentage for steelhead from Washington streams: (a) Snow Creek smolts, (b) Snow Creek adults, and (c) Forks Creek adults. Error bars represent 95% confidence intervals (2 SEs) around the mean scale-based age for all fish of a given parentage-assigned age. Solid line represents the 1:1 relationship. Coefficient of variation (CV) is the average of all CVs calculated for each individual within each group.
was probably due to differences in life history between hatchery and wild steelhead. Nearly all (352 of 361 fish; Table 1) of the adult Forks Creek steelhead used in the analysis of scale aging error were hatchery produced. Hatchery fish typically had less life history variation than wild fish (Dauer et al. 2009) because the hatchery spawns fish early in the season and rears them rapidly for release after one full year, whereas wild fish are spawned over a longer time period and commonly migrate as smolts after 2 years. The freshwater region of growth on the scale is the most difficult to read, so the simplification of this period greatly facilitates accurate reading. Length of fish was a significant factor in age match or mismatch (one-factor ANOVA: \( F = 7.39, df = 2, 360, \alpha = 0.05, P = 0.001 \)). Fish with ages that were underestimated by 1 year based on scale analysis tended to be larger (average length = 762 mm; marginally nonsignificant; Tamhane’s post hoc test: \( P = 0.092 \)) than fish with corroborated ages (666 mm) or overestimated ages (655 mm). The subtle bias that caused this somewhat paradoxical result is not obvious; one would have expected fish with underestimated ages to be smaller than average. It is possible that features of the fish and the scale itself caused the bias or that there was some bias in the reading. Some large fish that grow year-round in the ocean might have scales without an obvious annulus, which would lead to age underestimation. Misinterpretation of growth at the scale edge, especially if there is a lot of scale resorption, may also be a problem, especially for older fish (Chilton and Bilton 1986). All the fish in this category were 4- or 5-year-old hatchery fish; by comparison, the majority of hatchery fish were age 3. If these fish were marginal in body length (i.e., too long for a younger age-class but too small for an older age-class), the scale reader may have been reluctant to assign the older age biased by the marginal length. However, the body lengths were on both ends of the length–age distributions for both age-classes. Nevertheless, reluctance of the reader to assign older ages may be apparent in the trend shown in Figure 1c, where the age of 5-year-old fish was consistently underestimated. If such reluctance is the cause of this bias, then the bias could be eliminated if scale readers are blind to other information, such as length or population origin. However, these kinds of information are typically available to (or recommended for) agency scale readers (e.g., Minard and Dye 1998); having such information available presumably reduces or eliminates other types of errors.

**Repeat Spawning Error Rate**

Eighty-two Snow Creek adults were identified as repeat-spawning individuals (observed \( P_{\text{ID}} = 5.7 \times 10^{-5} \)); fish with identical genotypes were highly unlikely to be different individuals (\( P_{\text{ID, unbiased}} = 3.1 \times 10^{-23} \); \( P_{\text{ID, sibs}} = 5.5 \times 10^{-7} \)). Two of the 31 adults (6.5%; 95% CI = 0.79–20.26%) that were genetically identified as repeat spawners were not identified as repeat spawners by scale reading. One of these two adults was an unusual individual. It was first sampled as an out-migrant at 430 mm fork length, which is very large for a smolt and small for a jack. In salmonids, calcium from scales and bones is resorbed for use in restructuring the physical features upon maturation (e.g., elongated jaws and dorsal humps), resulting in the spawn check on scales. In this unusual fish, a spawn check either (1) was lacking during the first year in which the fish was sampled or (2) was missed by the scale reader; however, it is possible that the fish did mature. It is unknown whether fish that mature young have the same level of secondary sexual character development as older fish; it is also unknown whether spawn checks are present on the scales of fish that mature without going to sea. If we assume that this fish did not mature in the first year, then the error rate would be only 3%.

Fifty-one of 82 Snow Creek adult steelhead were identified as repeat spawners by checks on their scales but not by genetic analysis. We could not assess errors for these fish because we could not rule out the possibility that these fish returned and spawned without being sampled. We know that in some years, many adult fish were not sampled due to very high flows that compromised the weir. It is also possible that genotyping error in one or both of the samples from the same fish in different breeding seasons caused this discrepancy. However, our estimate of genotyping error was too low for this to be a substantial problem (0.6%; Seamons et al. 2004). These results therefore imply (but do not demonstrate) that some of the fish were incorrectly classified as repeat spawners based on scale analysis.

**Management Implications**

Our estimated error rate for scale-based ages was similar to those from previous studies of steelhead and other salmonids. For steelhead of the Hood River, Oregon, parentage- and scale-based ages differed in 2 (1.1%) of 175 wild summer-run (freshwater-maturing) adults and 81 (8.6%) of 942 wild winter-run adults (H. Araki, Swiss Federal Institute of Aquatic Science and Technology, personal communication). Among wild summer-run steelhead adults sampled from Little Sheep Creek, Oregon, parentage- and scale-determined ages differed for 8 (42%) of 19 fish (E. Berntson, National Oceanic and Atmospheric Administration,
personal communication). For spring Chinook salmon *O. tshawytscha*, Copeland et al. (2007) reported that the overall accuracy of scale-determined ages was 81.8%.

Errors associated with aging may have management implications. Steelhead age structure and life history are used by WDFW in models to predict returns and set harvest goals with co-managers in many river basins (B. Leland, WDFW, personal communication). Aging errors tend to smooth age structure, inflating weak cohorts and decreasing strong cohorts (Campana 2001). Aging errors may inflate smolt-to-adult return rates for weak cohorts, ultimately leading to inflated harvest goals (Copeland et al. 2007). As of 2007, there were 11 steelhead Distinct Population Segments listed as threatened or endangered under the U.S. Endangered Species Act (NOAA–NMFS 2007). Extinction risks are commonly calculated as part of the management process (McElhany et al. 2000). Aging errors may lead to overly optimistic estimates of population parameters and erroneously low extinction probabilities for endangered populations (Zabel and Levin 2002).

**Summary**

A recent review reiterated a recommendation to evaluate accuracy of age data (Maceina et al. 2007). Here, parentage data revealed that scale analysis was associated with low error rates in estimating the ages of wild steelhead smolts and hatchery adults and the spawning history of wild adults. The error rate was higher for the scale-based aging of wild adults, probably due to their complex life history. Accurate estimates of age structure are necessary for proper management of fish populations (Copeland et al. 2007), and scale analysis appears to be an appropriate method for estimating total age. Because obtaining the parentage data was neither easy nor inexpensive, our method of validation is not necessarily one that agencies should regularly implement; however, this method can be used when sufficient data are available. There is a certain amount of subjectivity to determining age based on scales, and thus it is likely that some error exists in all readings. Because aging error can affect management and conservation decisions, efforts should be taken to estimate this error by tagging, genetic analysis, or other techniques and to account for it in management decisions that hinge on age structure and the rate of repeat spawning.

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