Comparison of Methods Used to Age Spring–Summer Chinook Salmon in Idaho: Validation and Simulated Effects on Estimated Age Composition

Timothy Copeland,* Matthew W. Hyatt,[1] and June Johnson

Idaho Department of Fish and Game, 1414 East Locust Lane, Nampa, Idaho 83686, USA

Abstract.—Validation of aging methods with known-age individuals is rarely done with wild fish. We used samples collected from carcasses of adult Chinook salmon *Oncorhynchus tshawytscha* that were tagged as juveniles to (1) compare accuracy and precision of ocean ages determined from scales and fin rays and (2) simulate the effects of aging errors on run reconstruction (assignment to migratory cohort) under two age composition scenarios. Scale age had an overall accuracy of 81.8% and was biased high ($\chi^2 = 8.67$; $P = 0.014$). Fin ray age had an overall accuracy of 98.6% and was unbiased ($\chi^2 = 2.00$; $P = 0.34$). Precision of fin ray readings was higher than that of scale readings (coefficient of variation = 2.1% versus 7.8%, respectively). Accuracy of fin ray ages was greater than that of scale ages ($Z = 2.198$; $P = 0.03$). For two age composition scenarios, age classification errors were greatest when using scales and least when using fin rays. Aging errors inflated the size of weak cohorts in simulated run reconstructions. We showed how this can cause large errors in estimates of smolt-to-adult return rate when run strength and age composition vary among years. The amount of error associated with scale aging then becomes problematic for tracking the status of both threatened and healthy salmon stocks. Data based on fin ray readings provided the most accurate, unbiased estimates of age structure. Correction for methodological bias is important if age data are to be used in rigorous analyses.

Valid age data are integral to the understanding and management of fish populations. An assortment of techniques and structures has been used to estimate fish age (Boehlert 1985; Chilton and Bilton 1986; Lai et al. 1987; Stevenson and Campana 1992); success has varied depending on the technique and species of fish. Accurate age information is an essential tool for the management and recovery of the spring and summer runs of Chinook salmon *Oncorhynchus tshawytscha* that return to the Snake River basin (Kiefer et al. 2004). Age data are used for assigning mature Chinook salmon to cohorts, which allows calculation of survival and replacement rates, both important recovery criteria. Fin rays and scales have been used to estimate the age of Pacific salmon species (Bilton and Jenkinson 1969; Jearld 1983), but neither method has been validated for spring and summer Chinook salmon returning to the Snake River basin. Beamish and McFarlane (1983) recommended that age estimation methods be tested for accuracy by an accepted age validation technique (e.g., identification of known-age fish) before they are adopted. Failure to validate a technique may lead to

the use of inaccurate age data, resulting in serious errors in the management of a fish population.

Beamish and McFarlane (1983) defined validation as proving the accuracy of a technique. Aging error can exist in two forms: (1) error that affects accuracy, or the proximity of the age estimate to the true value, and (2) error that affects precision, or the reproducibility of individual measurements on a given structure (Campana et al. 1995). An ideal age reference collection contains structures of known age, thus allowing tests of both accuracy and precision (Campana et al. 1995). In practice, known-age samples from wild fish are rarely available (Campana 2001). As a result, most investigators of age estimation methods are forced to argue validity based on analysis of aging consistency within and between readers.

The initial impetus for this research was the mismatch between ages determined from scales and known ocean ages of Chinook salmon tagged as juveniles. Otoliths were considered as an alternative aging structure but proved to be opaque and impossible to clear (also see Chilton and Bilton 1986). Samples from adult spring–summer Chinook salmon carcasses collected by the Idaho Department of Fish and Game during 1999–2003 include scales and fin rays from individuals tagged with passive integrated transponder (PIT) tags as juveniles, providing the opportunity for critical analysis of both scale and fin ray aging methods. Because the number of known-age fish

* Corresponding author: tcopeland@idfg.idaho.gov
[1] Present address: Grant County Public Utility District, Post Office Box 878, Ephrata, Washington 98823, USA.

samples was not high in any particular year, we explored the implications of aging errors by simulation. Therefore, the objectives of this study were to (1) validate the use of annuli counts from scales and fin rays to determine whether these two structures provide accurate estimates of ocean age for Snake River spring and summer (SRSS) Chinook salmon; (2) determine which aging structure is more accurate for estimating the ocean age of SRSS Chinook salmon; and (3) simulate the effect of aging error from the two aging methods on run reconstruction (i.e., assignment of individuals to migratory cohorts). For the last objective, we demonstrate the probable effects of aging errors on the smolt-to-adult return (SAR) rate, a survival statistic of great interest to salmon managers. For the purposes of monitoring age composition of adult SRSS Chinook salmon, researchers rely solely on the ocean age of the fish because most juveniles migrate after one winter in freshwater habitat (Kiefer et al. 2002); therefore, we focus exclusively on ocean age.

Methods

Collection and preparation of scales and fin rays.— Scale and fin ray samples from Chinook salmon carcasses were collected from hatchery-reared and wild fish of known age. These known-age samples were obtained from mature salmon that had been marked as juveniles by implanting a PIT tag into the abdominal cavity of each fish. This tagging has been conducted since the early 1990s by other investigators to track survival and migration timing. Hatchery-reared fish were tagged before their release as juveniles, whereas wild fish were captured and tagged at smolt traps as the fish migrated downstream from their natal streams. After emigration from freshwater, individuals from SRSS Chinook salmon stocks reside in the ocean for 1–4 years before returning to spawn (Copeland et al. 2004). Given low SAR rates in recent years (typically <3%) and the large size of our study area, we collected known-age samples opportunistically. Scale and fin ray samples from hatchery-reared fish were collected from postspawn adults that returned to one of the Chinook salmon hatcheries in Idaho. Samples from wild fish were collected from carcasses found on spawning grounds or from wild adults captured and spawned as part of a supplementation study (Bowles and Leitzinger 1991). Samples from both hatchery and wild fish were collected in all years of the study.

Sample collectors were instructed to remove 10 scales and a portion of the dorsal fin (rays 2–6) from each fish. Scales were collected from the second and third scale rows above the lateral line, along or near the diagonal scale row extending from the posterior

insertion of the dorsal fin to the anterior insertion of the anal fin. The dorsal fin was held at a 90° angle to the body and was removed by making a subcutaneous cut across the fin below the base of the rays at the proximal ends of the pterygiophores while pulling upward. This procedure retained the base of the fin rays for sectioning. Fin rays were preserved by freezing until they were processed in the laboratory.

Aging structures were prepared and read in the laboratory. Scales were pressed onto acetate diacetate strips and viewed with a microfiche reader at 40× magnification. Fin rays were thawed, air dried in a fume hood, and coated in clear epoxy. Each fin ray was cut perpendicularly beginning at the base with a 0.3-mm, diamond-grit blade. Individual sections (1.3 mm thick) were fixed to standard glass microscope slides with a clear mounting medium and read with a compound microscope at 40× magnification.

Methodology comparisons.—We were limited by the number of known-age fish and continuity of readers; therefore, we used three data sets to address our objectives. We drew all known-age-.1 and age-.3 samples from our archive of samples collected during 1999–2003 ($n = 15$ and 26, respectively). We randomly selected 30 age-.2 samples. This procedure yielded 71 known-age samples with scales (first data set). Of these samples, 65 had fin rays that were already read (second data set). The third set of data were fin rays from known-age fish ($n = 73$) collected in 2004. To maintain continuity among readers for comparison of reader precision and bias between methods, we compared scale readings from the 1999–2003 samples with fin ray readings from the 2004 sample. To characterize and compare the overall accuracy of each method, we used the 1999–2003 samples for both methods.

Two trained readers independently assigned ages for each structure without reference to fish length. When fin rays are viewed under transmitted light, translucent zones represent annuli (Ferreira et al. 1999). Ocean annuli are broad, whereas freshwater annuli are narrow and bright. The criterion for scale annuli was cutting over of circuli that was consistent on both sides of the scale. Viewers only counted annuli laid down after rapid ocean growth had begun. For comparisons between structures, we derived final age assignments for each structure. When age assignments from the two readers were in agreement, this age was accepted as the final age. When disagreements between readers occurred or when the assigned age was judged unusual for the length of the fish, a third experienced reader was brought in and a collaborative reading session with all three participants was conducted until a final age for the structure was agreed upon. Structures deemed unreadable or structures for which no final age assignment
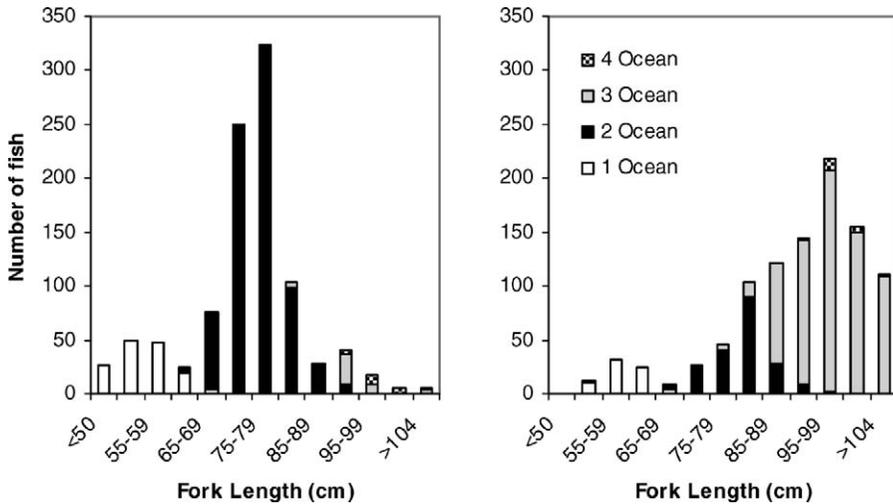
FIGURE 1.—Age composition in relation to length of Snake River spring and summer Chinook salmon used in simulation analysis: scenario 1 (left panel) represents a run of primarily age-.2 individuals; scenario 2 (right panel) represents a run of primarily age-.3 fish. Simulated populations ($N = 1,000$ fish) were based on proportions of wild adults passing Lower Granite Dam in 2000 and 2003 (Kiefer et al. 2002; Copeland et al. 2004). Each bar represents a 5-cm-length group, except individuals less than 50 cm were combined into one group and those greater than 104 cm were combined into another. For space reasons, only labels for every other 5-cm group are listed on the *x*-axis of each scenario.

could be agreed upon during the collaborative reading session were removed from further analysis.

Age frequency tables (Campana et al. 1995) were constructed to detect systematic differences in ages of matched structures. Age frequency tables summarize paired age comparisons and allow visual identification of systematic bias. We tested for consistent trends using a χ^2 test for symmetry (Hoenig et al. 1995).

Precision was measured by calculating the mean coefficient of variation (CV), as recommended by Chang (1982), using the formula

$$CV = 100 \times \frac{1}{N} \sum_{j=1}^{N} \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R - 1}}}{X_j},$$

where N is the number of fish aged, R is the number of times a fish was aged, X_{ij} is the ith age estimate for the jth fish, and X_j is the average age determined for the jth fish. As given, this formula provides an estimate of precision. When X_{ij} is assigned age and X_j is the true age, this formula calculates an estimate of percent bias.

Comparison of aging methods.—Direct comparison of ages based on scales versus fin rays was done for the 1999–2003 samples, although different readers were used for scales and fin rays. Accuracy of ages based on each structure was calculated by dividing the number of samples aged correctly by the number read for each age-group. These calculations provided the proportion

of each group of known-age fish that was aged correctly using each method. Samples that could not be aged by consensus were counted as errors for this analysis. We used a testing procedure analogous to χ^2, the two-tailed Z-distribution (Zar 1999), to test for differences among the proportions of correct ages between the two aging structures. Significance was assessed using an α-value of 0.05.

Simulations.—We used simulations to explore the implications of the errors that would result when using each structure for age assignments. We developed two simulated populations of Chinook salmon representing runs with two distinct age compositions based on recent observations from video recordings at Lower Granite Dam and carcass surveys. Scenario 1, derived from the 2000 run (Kiefer et al. 2002), represented a run that contained primarily age-.2 individuals; scenario 2, derived from the 2003 run (Copeland et al. 2004), represented a run consisting of a large proportion of age-.3 fish. Those age proportions were applied to a population of 1,000 fish for each scenario. Hereafter, these two populations (Figure 1) are referred to as the "true" populations.

We applied the accuracy rates associated with the two aging structures to examine the effect of misclassification on assigning ages to a typical run. The errors associated with ages based on each structure were measured as described above. The actual age composition was adjusted by these error rates to

TABLE 1.—Number of Snake River spring and summer Chinook salmon aged by three readings of scales and fin rays versus known ocean age (years). Samples were aged independently by two readers, and differences were resolved in a collaborative session. Samples that could not be aged by consensus are excluded. Scales were collected in 1999–2003; fin rays were collected in 2004.

Known ocean age	Scale age				Fin ray age			
	.1	.2	.3	.4	.1	.2	.3	.4
Reader 1								
.1	10	5			10	1		
.2		25	3	1	3	55		
.3		2	17	2		1	3	
Reader 2								
.1	11	3			10			
.2	1	25	4		1	57	1	
.3		4	16	4		1	3	
Collaboration								
.1	11	4			10			
.2		24	5		1	58		
.3		1	19	2			4	

simulate their effects on estimated age composition. The adjusted number in each age-class was divided by the true number to get a percentage under- or overestimated. The number of misclassifications out of 1,000 was computed for each scenario.

To show the implications of aging errors in practical terms, we extended our simulation to compute an SAR rate for a cohort when run strength and age composition varied. For simplicity, we only considered the contributions of a cohort at ages .2 and .3 because these age-classes comprise the bulk of the reproductive individuals. We assigned ages to two consecutive returns and computed the SAR for the age-.2 component of the first run. Aging errors were simulated by using the adjustments discussed above as applied to returns of 1,000, 8,000, and 45,000 individuals (spanning the approximate range of recent run strengths for wild SRSS Chinook salmon; 8,000 is close to the median) for two consecutive years. We added the number of age-.2 fish in the first year to the number of age-.3 fish in the second year to calculate the adult return from the simulated migratory cohort for the true, scale, and fin ray categories. We used the true category to compute the number of smolts necessary to produce an SAR rate of 1%; we then divided the number in the scale and fin ray categories by smolt number to estimate SAR rates based on the two aging methods. We considered situations in which both years had a constant age structure (scenario 1) or different age structures (both combinations of scenarios 1 and 2).

Results

We used 71 known-age scale samples collected during 1999–2003 to examine bias and precision between readers. Readers could not assign ages to five samples, even in collaboration; these unreadable scales were not included in calculations. Scale ages were consistent between readers (75% agreement; $\chi^2 = 2.87$, df = 4, $P = 0.58$). Accuracy of ages based on scales for the two individual readers was 66.7% and 78.6% for age-.1 fish, 83.3% and 86.2% for age-.2 fish, 76.7% and 81.0% for age-.3 fish, and 76.5% and 80.0% for all ages combined (Table 1). Accuracy of collaborative age estimates was 73.3% for age-.1 fish, 82.8% for age-.2 fish, 86.4% for age-.3 fish, and 81.8% for all ages combined. Because the possible range of errors for an age-.1 fish was truncated (i.e., zero was not a possibility), one would expect that accuracy would be higher and bias insignificant for that age-group; we did not find this to be the case. Scale ages were consistently biased above true age ($\chi^2 = 8.67$, df = 3, $P = 0.014$). When known-age-.1 and age-.2 scales were aged incorrectly, the true ages were almost always overestimated by 1 year. For known-age-.3 scales, no systematic under- or overestimation of age was observed.

The same readers also aged 73 known-age fin ray samples collected in 2004. Ages based on fin rays were consistent between readers (95% agreement; $\chi^2 = 2.00$, df = 2, $P = 0.39$). Accuracy of ages estimated by the individual readers was 90.9% and 100.0% for age-.1 fish, 94.8% and 96.6% for age-.2 fish, 75.0% for age-.3 fish (both readers), and 93.2% and 95.9% for all ages combined (Table 1). The 75% error rate for age-.3 fish was from one assignment error among the four individuals of that age present in the 2004 fin ray sample. Accuracy of consensus age estimates was 100.0% for age-.1 fish, 98.3% for age-.2 fish, 100.0% for age-.3 fish, and 98.6% for all ages combined. Fin ray ages were not consistently biased ($\chi^2 = 2.00$, df = 1, $P = 0.34$).

Fin ray ages determined by our readers were more precise than scale ages. Scale age estimates had a CV of 7.8% between readers and a bias of 6.0% (collaborative read versus known age). Fin ray ages had a CV of 2.1% and a bias of 0.6%. These results show that ages obtained from fin rays were more precise than those obtained from scales when read independently or in collaboration. In addition, collaborative readings were more accurate than independent readings, regardless of the structure being aged.

Comparison of Aging Methods

For the purposes of determining which structure provided the most accurate age information, we

TABLE 2.—Ocean age (years) assignments based on scales and fin rays of known-age Snake River Chinook salmon collected in 1999–2003 ($n = 65$ fish). Scales and fin rays were not read by the same technicians. All ages were estimated during a collaborative reading session.

Known ocean age	Scale age				Fin ray age			
	.1	.2	.3	.4	.1	.2	.3	.4
.1	11	4			13	1		
.2[a]		24	5		1	28	1	
.3[b]			1	19	2		1	21	1

[a] For scales, one sample not readable.
[b] For scales, four samples not readable.

confined our analysis to collaborative readings only. There were 65 samples collected during 1999–2003 with both scale and fin ray ages (not estimated by the same readers). For scales, there were 11 age assignment errors and four samples without a consensus reading (Table 2). For fin rays, all readings were resolved to a consensus age, and five assignment errors were made (Table 2). Accuracy rates were significantly higher for fin rays than scales (92.3% versus 76.9%; $Z = 2.1978$; $P = 0.03$). Accuracy of ages was lower for the 1999–2003 fin rays (92.3%) than for the 2004 samples (98.6%).

Simulations

We conducted two simulations to examine the potential effects of aging errors on age assignments under different age compositions. We used the error rates determined from the 1999–2003 samples for these simulations (Table 3). Because we did not have any known-age-.4 samples, we used the age-.3 aging accuracy and assumed that all errors would be underestimates. For scenario 1 (simulated high proportion of age-.2 fish), age assignments based on scale reading underestimated the number of age-.1 fish by 26.4%, underestimated the number of age-.2 fish by 12.2%, overestimated the number of age-.3 fish by

TABLE 3.—Error rates (%) used to adjust age composition for simulations of the effect of aging errors on Snake River Chinook salmon run reconstruction. Percentages were estimated from 1999–2003 data. Percentages for age-.4 fish were estimated from age-.3 data, assuming that all errors would be underestimates.

Known ocean age	Scale age				Fin ray age			
	.1	.2	.3	.4	.1	.2	.3	.4
.1	73.3	26.7			92.9	7.1		
.2		82.8	17.2		3.3	93.4	3.3	
.3		4.5	86.4	9.1		4.3	91.4	4.3
.4			13.6	86.4			8.6	91.4

TABLE 4.—Comparison of the true number at age in simulated populations ($N = 1{,}000$ fish) of Snake River spring and summer Chinook salmon and the adjusted numbers based on error rates from scale and fin ray aging methods: scenario 1 represents a run of primarily age-.2 individuals; scenario 2 represents a run of primarily age-.3 fish. Simulated populations were based on proportions of wild adults passing Lower Granite Dam in 2000 and 2003 (Kiefer et al. 2002; Copeland et al. 2004). Numbers in parentheses are errors expressed as percentages of true numbers at age.

Ocean age	True number at age	Adjusted number at age	
		Scales	Fin rays
Scenario 1			
.1	148	109 (−26.4)	163 (10.1)
.2	785	689 (−12.2)	746 (−5.0)
.3	47	180 (283.0)	71 (51.1)
.4	20	22 (10.0)	20 (0.0)
Scenario 2			
.1	71	51 (−28.2)	72 (1.4)
.2	200	218 (9.0)	224 (12.0)
.3	709	649 (−8.5)	654 (−7.8)
.4	20	82 (310.0)	50 (150.0)

283.0%, and overestimated the number of age-.4 fish by 10.0% (Table 4). Age assignments based on fin ray reading underestimated the number of age-.2 fish by 5.0%, overestimated the number of age-.1 fish by 10.1%, overestimated the number of age-.3 fish by 51.1%, and perfectly estimated the number of age-.4 fish. For this scenario, 182 and 63 classification errors were made by scale and fin ray age assignments, respectively.

For scenario 2 (simulated high proportion of age-.3 fish), age assignments based on scales underestimated the number of age-.1 and age-.3 fish by 28.2% and 8.5%, respectively (Table 4). Scale age assignments overestimated the number of age-.2 and age-.4 fish by 9.0% and 310.0%, respectively. Age assignments based on fin rays overestimated the number of age-.1 fish by 1.4%, age-.2 fish by 12.0%, and age-.4 fish by 150.0%; the number of age-.3 fish was underestimated by 7.8%. For this scenario, 152 and 80 classification errors were made by scale and fin ray age assignments, respectively.

We used the distribution of errors from Table 4 to assign ages to two consecutive runs and calculate an SAR estimate assuming several circumstances (Table 5). This part of the exercise involved only 21 permutations because some would have been redundant (e.g., two consecutive runs of 8,000 with large age-.3 components would yield results identical to those of a constant age structure dominated by age-.2 fish).

As changes to run strength and age structure between years became more extreme, aging error had

TABLE 5.—Snake River Chinook salmon cohort abundance and estimated smolt-to-adult (SAR) return rates under several scenarios of varying run strength (weak = 1,000; median = 8,000; strong = 45,000) and age composition (primarily age .2 or .3) in two consecutive years. Cohort abundance was the sum of age-.2 fish in year 1 and age-.3 fish in year 2. Number of smolts required to produce a true SAR of 1% was divided into cohort abundance to estimate SAR based on scale and fin ray ages.

Run strength/ age composition		Cohort abundance			Estimated SAR	
Year 1	Year 2	True	Scales	Fin rays	Scales	Fin rays
Weak .2	Weak .2	832	869	817	1.04	0.98
Weak .2	Weak .3	1,494	1,338	1,400	0.9	0.94
Weak .3	Weak .2	247	398	295	1.61	1.19
Weak .2	Median .2	1,161	2,129	1,314	1.83	1.13
Mean .2	Strong .2	8,395	13,612	9,163	1.62	1.09
Weak .2	Strong .2	2,900	8,789	3,941	3.03	1.36
Strong .2	Median .2	35,701	32,445	34,138	0.91	0.96
Median .2	Weak .2	6,327	5,692	6,039	0.9	0.95
Strong .2	Weak .2	35,372	31,185	33,641	0.88	0.95
Weak .2	Median .3	6,457	5,881	5,978	0.91	0.93
Median .2	Strong .3	38,185	34,717	35,398	0.91	0.93
Weak .2	Strong .3	32,690	29,894	30,176	0.91	0.92
Strong .2	Median .3	40,997	36,197	38,802	0.88	0.95
Median .2	Weak .3	6,989	6,161	6,622	0.88	0.95
Strong .2	Weak .3	36,034	31,654	34,224	0.88	0.95
Weak .3	Median .2	576	1,658	792	2.88	1.38
Median .3	Strong .2	3,715	9,844	4,987	2.65	1.34
Weak .3	Strong .2	2,315	8,318	3,419	3.59	1.48
Strong .3	Median .2	9,376	11,250	10,648	1.2	1.14
Median .3	Weak .2	1,647	1,924	1,863	1.17	1.13
Strong .3	Weak .2	9,047	9,990	10,151	1.1	1.12

an increasing effect on SAR estimation. When run strength and age structure were the same in consecutive years, the estimated SAR values were very close to the true values (Table 5; scale-based estimates: 4% higher than the true value; fin ray-based estimates: 2% lower than the true value). When run strength was held constant but age structure changed, the estimated SAR was low if the second run was dominated by age-.3 fish (Table 5; scales: 10% lower; fin rays: 6% lower). When the first run was dominated by age-.3 fish, the SAR of the age-.2 cohort in that first run was overestimated (Table 5; scales: 61% higher; fin rays: 19% higher) because it was bolstered by aging errors on the stronger, subsequent cohort.

Changes in run strength magnified aging error bias. For example, when run strength went from average (8,000) to strong (45,000), SAR biases were +62% for scale-based estimates and +9% for fin ray-based estimates. When a strong run was followed by an average run, biases were −9% for scale-based estimates and −4% for fin ray-based estimates (Table 5). Bias effects were larger when the two runs in question were weak (1,000) and average; for example, when a weak run was followed by a strong run, the estimated SAR values were +83% for scale-based estimates and +13% for fin ray-based estimates (Table 5). The greatest biases occurred when run strength changed in concert with a change in age structure from a primarily age-.3 run to a primarily age-.2 run. In this case, a change in

run strength from weak to average generated biases of +188% for scale-based estimates and +38% for fin ray-based estimates (Table 5). That is, the SARs estimated from the scale data exceeded the actual value threefold. We also repeated the simulation exercise under the assumption that the true SAR rate was 3% (data not shown). The estimated SARs and associated biases were proportionally greater: for example, if a particular age composition and run strength combination produced an estimated SAR of 2% when the true value was 1%, that combination resulted in an estimated SAR of 6% when the true value was 3%.

Discussion

We found that accuracy differed between scale and fin ray ages for Chinook salmon. Assignments based on fin rays were highly accurate (98.6%) and unbiased. Ages from scale readings were not as accurate (81.8%) and tended to be biased high. These results agree with Buckmeier's (2002) finding that accuracies less than 90% yield biased age estimates. Our fin ray ages were more accurate than those of Chilton and Bilton (1986; 91% accuracy), but we confined our analysis to ocean age only, whereas Chilton and Bilton (1986) determined total age (i.e., freshwater plus ocean ages). Published accuracies of ages based on scales validated with known-age Chinook salmon range from 75% (Godfrey et al. 1968) to 83% (Bilton et al. 1983); therefore, our scale age accuracy was typical for large-

scale, multistock studies (but see Flain and Glova [1988] for a more spatially restricted example). Our readers were very consistent in examining both structures, but scale ages were biased. Fin ray ages were not biased, as was also found by Chilton and Bilton (1986).

Chilton and Bilton (1986) found that their scale ages were biased low because of scale resorption and loss of annuli. However, in our study, scale ages were biased high. Godfrey et al. (1968) found that overestimation of ocean age was the most frequent error in scale ages and that this was linked to longer freshwater residence. Chilton and Bilton (1986) examined fish that spent a maximum of 1 year in freshwater. Spring and summer Chinook salmon in Idaho may spend one to two winters in freshwater (Kiefer et al. 2002). The harsh weather and long juvenile migration endured by SRSS Chinook salmon should increase the likelihood of growth checks and false annuli. Indeed, irresolvable differences in age assignments among readers were found only in scales. We speculate that this problem with scales may be common in stream-type Chinook salmon or other salmonids with an extended freshwater phase.

Ages based on fin rays were more precise among readers than were scale ages. All differences in fin ray ages between readers were resolved. However, precision computations did not account for unreadable samples. These were most prevalent in scales; therefore, the actual difference in precision between ages obtained from each structure was probably larger than the calculated values shown. The impact of precision depends on age composition (Campana 2001). The abbreviated age composition of Chinook salmon necessitates greater precision because of the magnitude of a 1-year error relative to life span.

Implications of Aging Errors

The effect of errors in age assignments for Chinook salmon will vary depending on age composition of the run. The simulation results showed that some errors offset each other; however, in both scenarios the dominant cohort lost more than it gained. Similarly, Worthington et al. (1995) showed that errors smooth the age distribution. Because one cohort tends to dominate the annual return of SRSS Chinook salmon in most years, the effect of aging errors will be to inflate the SAR estimates of weak cohorts and reduce those of strong cohorts. Zabel and Levin (2002) demonstrated how aging errors in salmon can inflate cohort productivity estimates, smooth variances, and ultimately translate into management effects (e.g., inflated harvest goals).

Errors in parameters derived from age distributions can result even if the aging method is unbiased, but these biases can be corrected if the error structure is known (Barlow 1984). The 1999–2003 samples gave conservative error rates for use in the simulations of fin ray ages because the random draw from the age-.2 archive yielded more samples with reading errors than are typically found in a single year (e.g., 97% by Kiefer et al. [2004] versus 92.3% from our 1999–2003 fin ray samples). The use of an archive like ours should increase accuracy and consistency by providing a consistent source of standards for reference and for the training of new readers (Campana 2001).

Sampling error can inflate inaccuracies (Worthington et al. 1995). Therefore, smaller sample sizes (relative to population size) will mandate use of the most accurate method available. However, the tradeoff of accuracy and precision versus cost must also be weighed. Given the threatened status of SRSS Chinook salmon, we believe that the extra effort required for fin ray analysis is warranted, particularly as data are parsed into local populations (see Interior Columbia Basin Technical Recovery Team, unpublished 2003 report [available at www.nwfsc.nooa.gov/trt]). If errors are generated by freshwater checks, scale bias will occur even if samples are taken before the fish die (e.g., during dam passage).

We demonstrated that aging errors can have an important influence on estimated SAR values. This effect is exacerbated by differences between years in abundance and age structure. Proportional biases were always greater when one of the runs in question was weak (i.e., proportional effects of aging errors will be greatest when adult abundances are low); hence, one strong cohort could artificially raise the SAR values estimated for the preceding and subsequent weaker cohorts. Because the artificial deflation of a strong cohort is proportionally less important than the inflation of weak cohorts (i.e., a few additions will be much more important if year-class strength is low), over time the mean SAR values will probably be inflated because of aging errors. The amount of error associated with scale aging then becomes problematic for tracking the status of threatened stocks. Because the effect of aging errors on absolute SAR values was proportional to the real value, such errors also should be of concern for the management of healthy stocks (i.e., those with higher absolute SAR values).

Validation of age assignments is of utmost importance in fisheries biology (Beamish and McFarlane 1983). Release and recapture of marked fish, as we have done here, is the most rigorous means of age validation (Campana 2001). We continue to update and use our known-age archive for training and reference. Although the use of multiple readers reduces errors (Buckmeier 2002), validation should be an ongoing

process. The simplified age structure of Chinook salmon reduced the potential magnitude for age errors (in an absolute sense) relative to that of species with longer life spans. However, errors were still present, and their proportional effect can be large; therefore, it is important to reduce or to account for them if the data are to be used in rigorous analyses.

Conclusions

Use of wild fish for age validation with known-age individuals is rare (Campana 2001). We have provided some estimates of error structure, thus enabling corrections to be incorporated into computations of parameters derived from the age structure of Chinook salmon. However, our research has found growth differences in time and space (Copeland et al. 2005); therefore, aging error structure should be updated regularly on a population-specific basis. Environmental and life history characteristics can affect aging bias, especially when scales are used. Implications of these errors will depend on age structure of the population of interest but will tend to inflate survival estimates when abundance and age structure fluctuate.

Of the aging methods we examined, fin rays provided the most accurate, unbiased estimates of age structure. Scales also gave reproducible results, but scale ages were consistently biased. Correction of errors in age assignments based on fin ray ages is likely to be the most straightforward. Collaborative reading sessions are worthwhile, regardless of aging structure. Aging errors in the presence of changing abundance and age composition will cause mean survival estimates to be biased upward.

References

Barlow, J. 1984. Mortality estimation: biased results from unbiased ages. Canadian Journal of Fisheries and Aquatic Sciences 41:1843–1847.

Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirement for fish age validation in fisheries biology. Transactions of the American Fisheries Society 112:735–743.

Bilton, H. T., M. Flain, F. Lucas, P. Kearton, and R. Gard. 1983. Tests on the accuracy of ageing New Zealand quinnat salmon (*Oncorhynchus tshawytscha*) from their scales. Canadian Technical Report of Fisheries and Aquatic Sciences 1199.

Bilton, H. T., and D. W. Jenkinson. 1969. Age determination of sockeye (*Oncorhynchus nerka*) and chum (*O. keta*) salmon from examination of pectoral fin rays. Journal of the Fisheries Research Board of Canada 26:1199–1203.

Boehlert, G. W. 1985. Using objective criteria and multiple regression models for age-determination in fishes. U.S. National Marine Fisheries Service Fishery Bulletin 83:103–117.

Bowles, E., and E. Leitzinger. 1991. Salmon supplementation studies in Idaho rivers (Idaho supplementation studies): experimental design. Idaho Department of Fish and Game Report to Bonneville Power Administration, Portland, Oregon.

Buckmeier, D. L. 2002. Assessment of reader accuracy and recommendations to reduce subjectivity in age estimation. Fisheries 27(11):10–14.

Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59:197–242.

Campana, S. E., M. C. Annand, and J. I. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society 124:131–138.

Chang, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Sciences 39:1208–1210.

Chilton, D. E., and H. T. Bilton. 1986. New method for aging Chinook salmon (*Oncorhynchus tshawytscha*) using dorsal fin rays, and evidence of its validity. Canadian Journal of Fisheries and Aquatic Sciences 43:1588–1594.

Copeland, T., J. Johnson, and P. R. Bunn. 2004. Idaho natural production monitoring and evaluation. Idaho Department of Fish and Game, Report 04-47, Boise.

Copeland, T., J. Johnson, and P. R. Bunn. 2005. Idaho natural production monitoring and evaluation. Idaho Department of Fish and Game, Report 05-38, Boise.

Ferreira, L. C. J., R. J. Beamish, and J. H. Youson. 1999. Macroscopic structure of the fin rays and their annuli in pectoral and pelvic fin rays of Chinook salmon *Oncorhynchus tshawytscha*. Journal of Morphology 239:297–320.

Flain, M., and G. J. Glova. 1988. A test of the reliability of otolith and scale readings of Chinook salmon (*Oncorhynchus tshawytscha*). New Zealand Journal of Marine and Freshwater Research 22:497–500.

Godfrey, H., D. D. Worlund, and H. T. Bilton. 1968. Tests on the accuracy of ageing Chinook salmon (*Oncorhynchus tshawytscha*) from their scales. Journal of the Fisheries Research Board of Canada 25:1971–1982.

Hoenig, J. M., M. J. Morgan, and C. A. Brown. 1995. Analysing differences between two age determination methods by tests of symmetry. Canadian Journal of Fisheries and Aquatic Sciences 52:364–368.

Jearld, A., Jr. 1983. Age determination. Pages 301–324 *in* L. A. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Kiefer, R. B., P. R. Bunn, and J. Johnson. 2002. Natural production monitoring and evaluation. Idaho Department of Fish and Game, Report 02-24, Boise.

Kiefer, R. B., J. Johnson, P. R. Bunn, and A. Bolton. 2004. Natural production monitoring and evaluation. Idaho Department of Fish and Game, Report 03-30, Boise.

Lai, H. L., D. R. Gunderson, and L. L. Low. 1987. Age-determination of Pacific cod, *Gadus macrocephalus*, using five aging methods. U.S. National Marine Fisheries Service Fishery Bulletin 85:713–723.

Stevenson, D. K., and S. E. Campana. 1992. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117.

Worthington, D. G., A. J. Fowler, and P. J. Doherty. 1995. Determining the most efficient method of age determination for estimating the age structure of a fish population. Canadian Journal of Fisheries and Aquatic Sciences 52:2320–2326.

Zabel, R. W., and P. S. Levin. 2002. Simple assumptions on age composition lead to erroneous conclusions on the nature of density dependence in age-structured populations. Oecologia 133:349–355.

Zar, J. H. 1999. Biostatistical analysis, 4th edition. Prentice-Hall, Upper Saddle River, New Jersey.