North American Journal of Fisheries Management 39:498–508, 2019

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10286

ARTICLE

Accuracy and Precision of Age Estimates Obtained from Three Calcified Structures for Known-Age Kokanee

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Abstract
Kokanee *Oncorhynchus nerka* growth is often density dependent; thus, proper management of kokanee populations necessitates an understanding of population dynamics using age structure data. To date, no calcified structures have been validated for kokanee. We compared the accuracy (i.e., the percentage of reconciled age estimates that matched the known ages of fish) and precision (i.e., the percentage of fish for which complete agreement was achieved on age estimates among all readers) of aging estimates for scales, sectioned otoliths, and sectioned pectoral fin rays from 455 known-age kokanee (ages 0–4) collected from five lentic waters in Idaho. Across all waters combined, mean weighted accuracy and precision were similar for scales (86% and 70%, respectively), fin rays (83% and 65%), and otoliths (82% and 65%), with no significant differences between structures. However, among water bodies, accuracy and precision of each calcified structure varied considerably. For example, scales were the most accurate and precise structure and otoliths were the least accurate and precise structure at one water body, while otoliths were the most accurate and precise structure and scales were the least accurate structure at two water bodies. Fin rays were the least precise structure at four of the five study waters, but were the least accurate structure for only one water body. Individual reader accuracy was most affected by fish age and water body, and older fish (age 3 and older) were consistently assigned incorrect ages regardless of the water body or the calcified structure. Taken collectively, all three structures produced satisfactory aging accuracy and precision for kokanee, but no structure was unequivocally best; at any individual water body, annual growth and local environmental conditions appeared to influence the readability of calcified structures.

Semelparous kokanee (landlocked Sockeye Salmon *Oncorhynchus nerka*) are a popular sport fish that generally reach maximum ages of 2–4 years (e.g., Rieman and Myers 1992; Grover 2005; Lepak et al. 2012). Kokanee are endemic to many lentic systems across the western United States and Canada, but state and provincial management agencies commonly use hatchery supplementation to introduce populations and maintain stocks for recreational harvest. In addition to providing high-yield harvest fisheries, kokanee may also serve as important forage fish for predatory species (e.g., Rainbow Trout *O. mykiss*, Lake Trout *Salvelinus namaycush*, and Bull Trout *Salvelinus confluentus*) in some trophy fisheries (Wydoski and Bennett 1981; Johnson and Martinez 2000; Hansen et al. 2010). In Idaho, kokanee are an integral part of numerous fisheries that generate high angler effort, thus making them a management priority in many waters (IDFG 2019).

Kokanee population management goals often seek to balance fish size, catch rates, and abundance. Kokanee populations exhibit strong density-dependent growth (Rieman and Myers 1992; Buktenica et al. 2007), which poses

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Received October 5, 2018; accepted March 26, 2019

a notable management quandary. At high densities, kokanee are smaller and often less desirable to anglers. At lower densities, kokanee are larger and their catchability by anglers is high (Rieman and Maiolie 1995), yet overall catch rates may be lower than anglers desire. Thus, angler preferences are important for establishing management goals. Furthermore, kokanee management is complicated in some waters by the presence of large predatory fishes that can influence kokanee abundance and growth (O'Gorman et al. 1987; Michaletz 1998; Ng et al. 2016). The competing and dynamic aspects of kokanee abundance and growth make the management of kokanee sport fisheries challenging.

The dual role of kokanee in many fisheries—serving as both a target fishery and as the prey base for trophy fisheries—has motivated extensive work to model their population dynamics and interactions with other species (e.g., McGurk 1999; Martinez et al. 2009; Hansen et al. 2010; Pate et al. 2014). Understanding the dynamic rate functions (i.e., growth, mortality, and recruitment) of a fish population is crucial for effective fishery management (Ricker 1975), and quantifying these functions usually requires the use of age structure data. Historically, kokanee age estimates were obtained through the analysis of length frequency data (Rieman and Myers 1992; Parkinson et al. 1994). However, length frequency analyses are less useful than hard structure age estimation because the lengths of age-classes overlap, especially for older fish (Rieman and Myers 1992; Parkinson et al. 1994; Maceina et al. 2007). More recently, age estimation using calcified structures has served as the standard technique for kokanee (e.g., Lepak et al. 2012; Ryan et al. 2014), but no calcified structures have been validated for this species. Without validation of calcified structures for estimating the age of kokanee, there is little consistency across studies, and the accuracy of age estimates is unknown.

In this study, we compared the accuracy and precision of two commonly used structures—scales and sectioned otoliths—for estimating the age of kokanee (Rieman and Myers 1992; Parkinson et al. 1994; Lepak et al. 2012; Ryan et al. 2014). In addition, we compared accuracy and precision of sectioned pectoral fin rays, which are known to provide reliable age estimates for other salmonid species (Chilton and Bilton 1986; Zymonas and McMahon 2009; Erhardt and Scarnecchia 2013). All fish were of hatchery origin and were of known age.

METHODS

Kokanee were collected from five lentic water bodies in Idaho by using experimental gill nets or midwater trawls (Table 1). Each water body receives annual hatchery supplementation, and all stocked kokanee were given an otolith thermal mass-mark (cold brand; Volk et al. 1990) during hatchery rearing to distinguish the hatchery fish from wild fish and to discern brood years for this evaluation. All kokanee were stocked in late May or early June as age-0 fish and were less than 100 mm at the time of stocking.

Sampling at Lake Pend Oreille occurred during the dark phase of the moon on September 1–4, 2013, using a standard midwater trawl sampling design (Rieman and Myers 1992). The trawl net measured 10.5 m long and consisted of graduated stretch-measure mesh to acquire individuals across the spectrum of available sizes. We towed the net through the water and covered the entire vertical distribution of kokanee. At the end of each haul, kokanee collected in the trawl net were bagged and placed on ice. Upon return to the laboratory, kokanee were stored in a deep freezer until they were thawed in warm water and processed.

Sampling at Devils Creek Reservoir, Lower Twin Lake, Mirror Lake, and Montpelier Reservoir occurred during the dark phase of the moon in June 2016 and June 2017. Fish were sampled using three experimental gill nets comprised of six mesh sizes placed in random order when manufactured. Net locations were randomly selected for each water body in 2016, and those same net locations were repeated in 2017. Gill nets were suspended at depth to cover the range of the thermocline and were fished

TABLE 1. Study site, surface area (ha), sample size (n), and TL (mm) statistics for kokanee that were sampled from five lentic water bodies in Idaho and used for age estimation (Min = minimum; Max = maximum). Samples from Lake Pend Oreille were collected in 2013; samples from all other sites were collected in 2016 and 2017.

				TL (mm)			
Study site	Surface area (ha)	Collection method	n	Mean	SD	Min	Max
Devils Creek Reservoir	50	Gill net	44	254	94	94	362
Lake Pend Oreille	32,900	Trawl	144	196	43	117	265
Lower Twin Lake	158	Gill net	128	263	59	90	357
Mirror Lake	34	Gill net	110	210	51	101	278
Montpelier Reservoir	53	Gill net	29	265	73	142	354

overnight. Sampled kokanee were placed on ice, and all fish processing occurred in the field.

Captured fish were measured to the nearest millimeter (TL), and hard structures were collected from each individual. Approximately 20 scales were removed from the area slightly posterior of the dorsal fin and above the lateral line on the left side of each fish (DeVries and Frie 1996). Pectoral fin rays were removed via the methods described by Koch et al. (2008), where the first three fin rays on the left side of the fish were cut off just below the surface of the skin. The entire fin was removed from smaller individuals (≤150 mm). Scales and pectoral fin rays were placed in coin envelopes labeled with a unique fish identification number. Both sagittal otoliths were extracted following the methods described by Schneidervin and Hubert (1986): an incision was made through the isthmus to remove the gill arches, and the bulla was snipped with scissors and pried open to expose the otoliths. The otoliths were removed, cleaned of excess tissue, and placed into labeled microcentrifuge tubes. All structures were allowed to air-dry for at least 2 weeks prior to processing.

After drying, scales from Lake Pend Oreille were rinsed and pressed onto acetate strips with a roller press (hereafter, "pressed scales"). Scales from all other water bodies were mounted between two microscope slides (hereafter, "mounted scales"). Pressed scales were viewed using a microfiche projector, whereas mounted scales were viewed under a compound microscope using reflected light at 25× magnification and the Image ProPlus image analysis system (Media Cybernetics, Silver Spring, Maryland).

Pectoral fin rays from all water bodies were mounted in epoxy following the method described by Koch and Quist (2007). Two cross sections (0.6–0.8-mm thickness) were cut near the base of each fin ray using a low-speed saw set at approximately 200 revolutions/min (Buehler, Inc., Lake Bluff, Illinois). Sections were viewed under a compound microscope using reflected light at 100× magnification.

One sagittal otolith from each fish was analyzed for thermal marks to determine the origin (i.e., hatchery or wild) and true age (as determined by the otolith thermal mark) of the fish. For all waters except Lake Pend Oreille, otoliths were mounted (with the sulcus facing down) to petrographic slides using Crystalbond (Aremco). Once the Crystalbond hardened, the otolith was gently sanded (with only a few circular strokes) on 9-μm lapping film, rinsed, and viewed under a compound microscope with transmitted light at 200× magnification. This process was repeated until the thermal mark appeared, at which point the otolith was polished on finer, 3-μm lapping film with a few additional strokes to intensify the mark. Otoliths for which a thermal mark did not appear were considered of wild origin, and all structures from those fish were removed from the study. Otoliths collected from Lake Pend Oreille were processed similarly, but thermal marks were interpreted at the Washington Department of Fish and Wildlife's Otolith Laboratory.

The other sagittal otolith from each individual was mounted in epoxy and sectioned (0.6–0.8-mm thickness) through the nucleus along the transverse plane using the same low-speed saw as used for fin ray sectioning. Sectioned otoliths were viewed under a compound microscope using reflected light at 40× magnification. Thermals marks on otoliths were not visible to the readers while viewing sectioned otoliths.

All structures except pressed scales were aged by independent readers who viewed still images of each structure on a computer monitor. For four of the five water bodies, the same three readers interpreted age for all of the structures, but a different set of three readers interpreted age for Lake Pend Oreille fish. Prior to age estimation, each reader received formal training and reviewed several training samples to become familiar with annulus patterns on each structure. Annuli on pectoral fin rays and otoliths were identified as translucent bands separated by opaque areas (Hining et al. 2000; Schill et al. 2010; Buckmeier et al. 2017). Scale annuli were identified as crowding and cutting over of circuli (DeVries and Frie 1996; McInerny 2017). None of the readers had knowledge of fish length during aging efforts, and all readers had extensive experience in enumerating the annuli of various structures prior to the study. For any given structure where age agreement was not reached through independent examination, a reconciled age was assigned through joint examination by all three readers. Any fish with an individual structure from which age could not be interpreted due to structure deformity or poor processing was removed from the analyses for all structures.

To estimate the reliability of age estimates, age bias plots were constructed to evaluate the deviation in estimated age (reconciled among all readers) from the true age for each calcified structure using water body-specific and pooled data. We calculated accuracy of each structure as the percentage of reconciled age estimates from the structure that matched the known ages of fish. Precision in age estimates was assessed for each structure by enumerating the total number of instances in which complete agreement among all three readers was achieved and dividing that number by the total number of fish. We constructed 95% confidence intervals (CIs) around accuracy and precision estimates to infer statistical significance (i.e., nonoverlapping CIs). In addition, we calculated the coefficient of variation (CV; 100 × [SD/mean]) to measure the variation in age estimates among readers, and we calculated an average value for each structure (Chang 1982; Campana 2001). Weighted mean values of accuracy, precision, and CV were reported to summarize data across all water bodies while accounting for differences in sample size.

Logistic regression models were used to estimate the probability of assigning an age correctly; each reader of each structure for each fish was used as the experimental unit, with dummy values of 0 (incorrect age assignment) or 1 (correct assignment) used as the response variable. Eight a priori candidate models were fit to evaluate how water body, structure, and reader affected the probability of correctly assigning the age of a fish. Interaction terms were also included to evaluate whether the accuracy of a particular structure varied by reader and by water body. Akaike's information criterion corrected for small sample size (AIC_c) was used to evaluate the relative plausibility of each candidate model (Akaike 1973; Burnham and Anderson 2002). The change in AIC value (ΔAIC_c) from the top model is a measure of the support of each model relative to the most-supported model, with differences less than 2 suggesting substantially more support for a model. We also calculated AIC_c weights to provide a relative measure of support for each model in the candidate set. Models were only used to estimate the probability of assigning an age correctly and the factors affecting that process; they were not used to provide information on the variability of age estimates or the bias of age estimates (average difference from the true age). Lake Pend Oreille was excluded from this analysis because readers were not the same for that water body.

The 95% CIs around the coefficient estimates of the logistic regression models were estimated using profile likelihood methods (Zuur et al. 2009). As noted earlier, if the 95% CI around the coefficient estimate overlaps 1.0, then it can be assumed that there is no significant effect at the $\alpha = 0.05$ level. Models were fitted using R statistical software (R Development Core Team 2011).

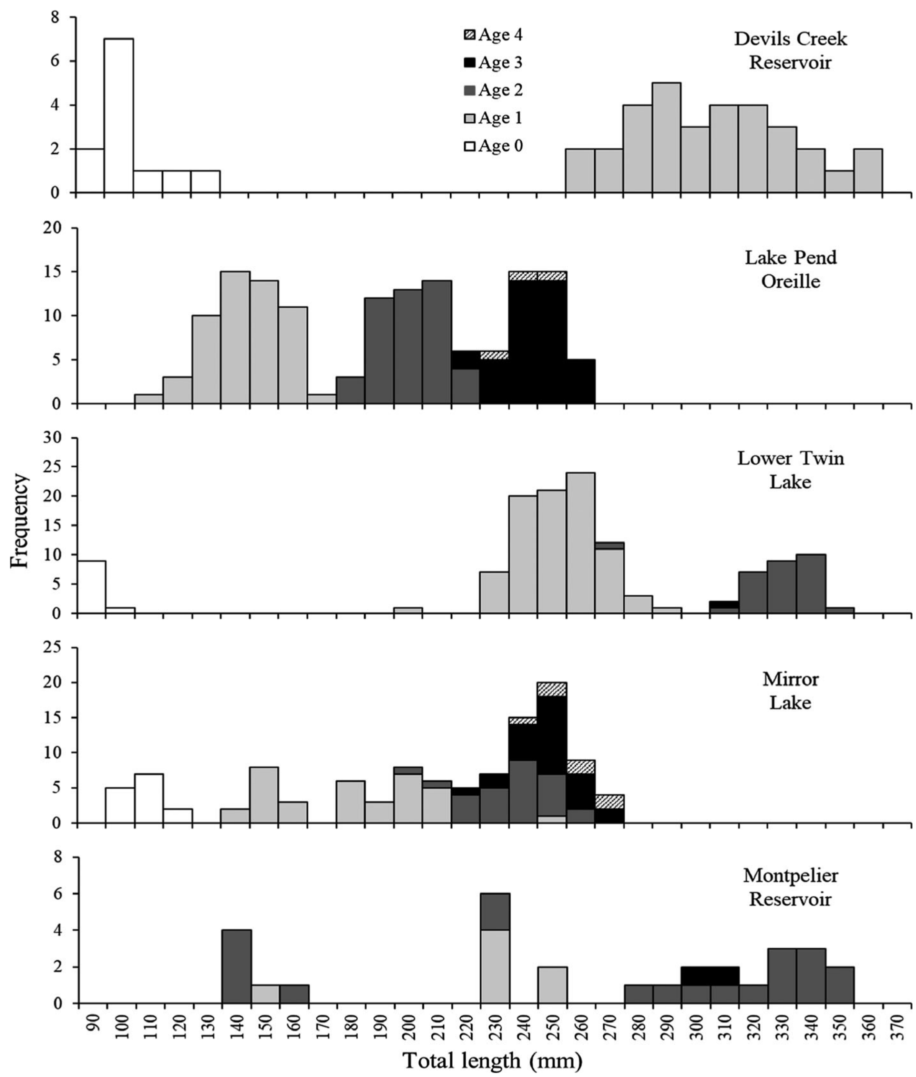

FIGURE 1. Length frequency distributions for 455 known-age kokanee sampled across five lentic water bodies in Idaho.

RESULTS

In total, we processed 503 kokanee for age estimation. Forty-eight fish were removed from this evaluation because at least one structure was unusable. True ages and age estimates for the remaining 455 fish varied from 0 to 4 years, and TLs were variable across water bodies, ranging from 90 to 362 mm (Table 1; Figure 1). Annual growth of kokanee was highest for Devils Creek Reservoir, although no known-age fish greater than age 1 were sampled there. Lake Pend Oreille and Mirror Lake exhibited the slowest growth of kokanee among the study waters (Figure 2).

Across all waters combined, accuracy and precision were slightly higher for scales (86% and 70%, respectively) than for sectioned pectoral fin rays (83% and 65%) and sectioned otoliths (82% and 65%), but 95% CIs overlapped for all comparisons, indicating no significant differences between structures (Table 2). Scales also exhibited slightly lower variability in age estimates (CV = 9.3%) than otoliths (CV = 10.7%) and fin rays (CV = 13.6%). Reconciled age estimates across all water bodies had a tendency to be slightly higher than the true age for age-1 kokanee and lower than the true age for age-3 and age-4 fish (Figure 3).

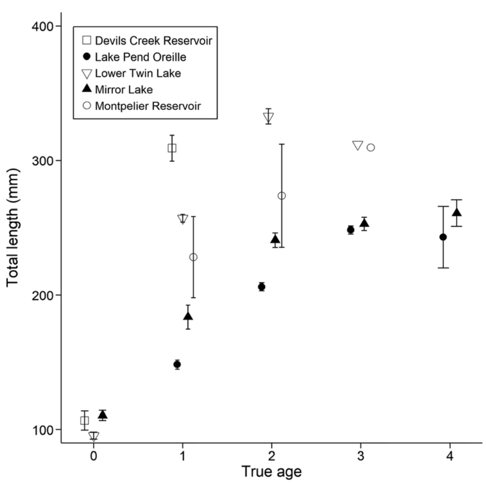

FIGURE 2. Average TLs of 455 known-age kokanee sampled from five lentic water bodies across Idaho. Error bars represent 95% confidence intervals.

Among water bodies, accuracy and precision of each calcified structure varied considerably (Table 2; Figure 4). For example, scales were the most accurate and precise structure and otoliths were the least accurate and precise structure for fish sampled from Lake Pend Oreille. However, otoliths were the most accurate and precise structure and scales were the least accurate structure for fish sampled at Montpelier Reservoir and Mirror Lake. Fin rays were the least precise structure at four of the five study waters but were the least accurate structure only for Lower Twin Lake.

The logistic regression model containing all parameters (i.e., the global model) had orders of magnitude more support than any other candidate model relating individual reader accuracy to factors affecting that accuracy (Table 3). However, besides the intercept, the only parameters with statistically significant coefficient estimates (meaning that the 95% CIs did not overlap 1.0) were water body, reader, and the true age of the fish (Table 4). Fish age had the largest effect on reader accuracy: mean individual reader accuracy was 99% for age 0, 86% for age 1, 72% for age 2, 54% for age 3, and only 10% for age 4. Across all structures combined, individual reader accuracy was over 50% higher for the water body with the highest overall accuracy (Devils Creek Reservoir; 97%) compared to the water body with the lowest overall accuracy (Montpelier Reservoir; 64%).

TABLE 2. Accuracy and precision of ages estimated by three readers for scales, sectioned otoliths, and sectioned pectoral fin rays from 455 known-age kokanee sampled from five lentic water bodies across Idaho. Accuracy indicates the frequency of reconciled age estimates matching known fish ages. Precision indicates the frequency of complete agreement among all three readers during independent age estimates. Mean coefficient of variation (CV) values were calculated from the independent age estimates. Means are presented with 95% confidence intervals (CIs).

	Scales			Otoliths			Pectoral fin rays		
Water body	Accuracy (%)	Precision (%)	CV (%)	Accuracy (%)	Precision (%)	CV (%)	Accuracy (%)	Precision (%)	CV (%)
Devils Creek Reservoir	100	91	3.9	100	98	2.0	100	86	6.9
Lake Pend Oreille	94	74	6.7	72	40	20.4	88	71	9.4
Lower Twin Lake	94	66	12.3	93	81	7.4	83	59	20.1
Mirror Lake	69	63	6.6	78	65	7.9	75	60	8.0
Montpelier Reservoir	62	66	12.0	76	76	10.4	66	48	30.9
Weighted mean (±95% CI)	86 ± 3.2	70 ± 4.2	8.3	82 ± 3.5	65 ± 4.3	11.3	83 ± 3.5	65 ± 4.4	13.2

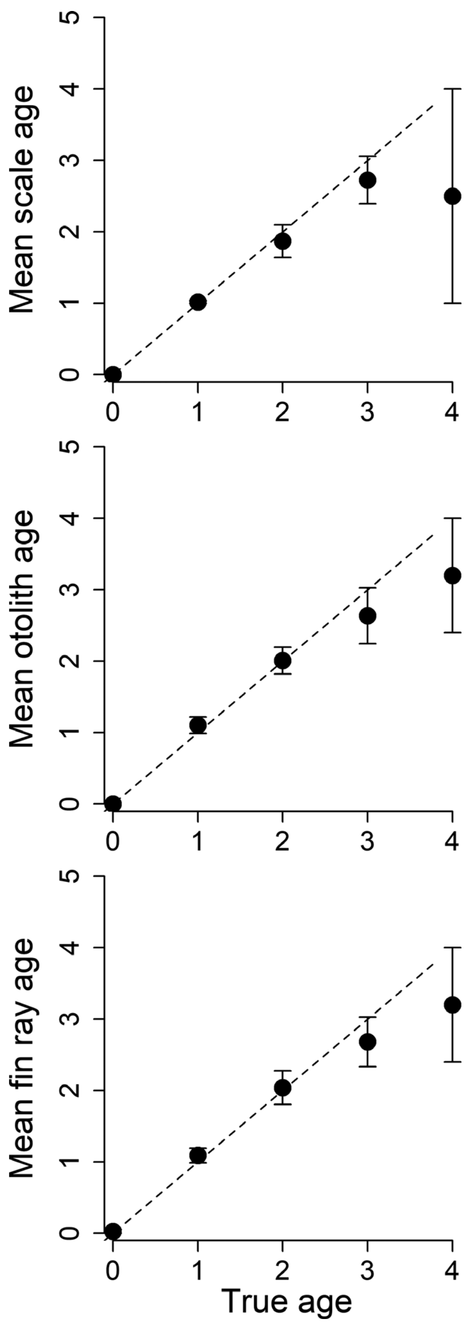

FIGURE 3. Relationships between true age (years) and mean reconciled age using scales, sectioned otoliths, and sectioned pectoral fin rays from 455 known-age kokanee sampled from five lentic water bodies in Idaho. Data points represent the estimated mean reconciled ages for each calcified structure relative to true age. Error bars represent root mean square error; the dashed line represents exact agreement.

DISCUSSION

No calcified structure was unequivocally superior for estimating kokanee age for the five populations in this study. We found that scales had the highest weighted mean accuracy and precision across all waters combined, but among individual water bodies, the most accurate and precise structure was usually otoliths. This disparity was driven in part by sample size being highest at Lake Pend Oreille, where scale aging accuracy and precision were very high and otolith aging accuracy and precision were comparatively low. The results at Lake Pend Oreille may have been influenced by differences in the scale preparation method (Gürsoy et al. 2005), but given the comparatively low accuracy from using otoliths and fin rays, we suspect that the results are driven by differences in reader experience with these structures. Indeed, the independent readers who interpreted ages for Lake Pend Oreille had exclusively used scales to estimate kokanee age for over 10 years as part of a long-term population monitoring program, but their experience with otolith and fin ray aging was considerably less extensive. In contrast, the readers who assigned ages to all other kokanee populations in our study did not have the benefit of such long-term population- and structure-specific experience.

Even with the exclusion of Lake Pend Oreille from the analyses, logistic regression results indicated significant differences in the accuracy of age estimation among readers and among water bodies. Accurate estimation of fish age is, in part, a function of reader experience and competency (McBride et al. 2005; Ross et al. 2005; Oele et al. 2015). However, regardless of reader experience, the formation of an annulus on any calcified structure is influenced by the environment (Schramm 1989; Beckman and Wilson 1995), which serves as another source of aging error. Most age validation studies using known-age fish have evaluated only one population (e.g., Buckmeier et al. 2002; Ross et al. 2005; Klein et al. 2017). In such instances, any comparison of the accuracy and precision of age estimates among calcified structures ignores the potential effect that the local environment may have on the ability to accurately assign ages to fish using various structures. Age assignments using scales from known-age Muskellunge *Esox masquinongy* sampled from five separate Wisconsin lakes demonstrated poor agreement with true age (accuracy = 32%; Fitzgerald et al. 1997), but the population origin was not retained in the analyses, and sample size was low ($n = 25$). We are aware of no study prior to ours that has explicitly evaluated differences in structure accuracy and precision among multiple water bodies by using known-age fish. The reader effect observed in the current study supports previous studies (McBride et al. 2005; Ross et al. 2005), but this effect essentially functions as a nuisance parameter in any aging study.

Considering the water body effect observed here, we are unable to definitively recommend a particular calcified structure to use for kokanee age estimation. All three structures produced satisfactory results for estimating ages of kokanee to some extent, but our data do not conclusively identify a particular structure to use across all water

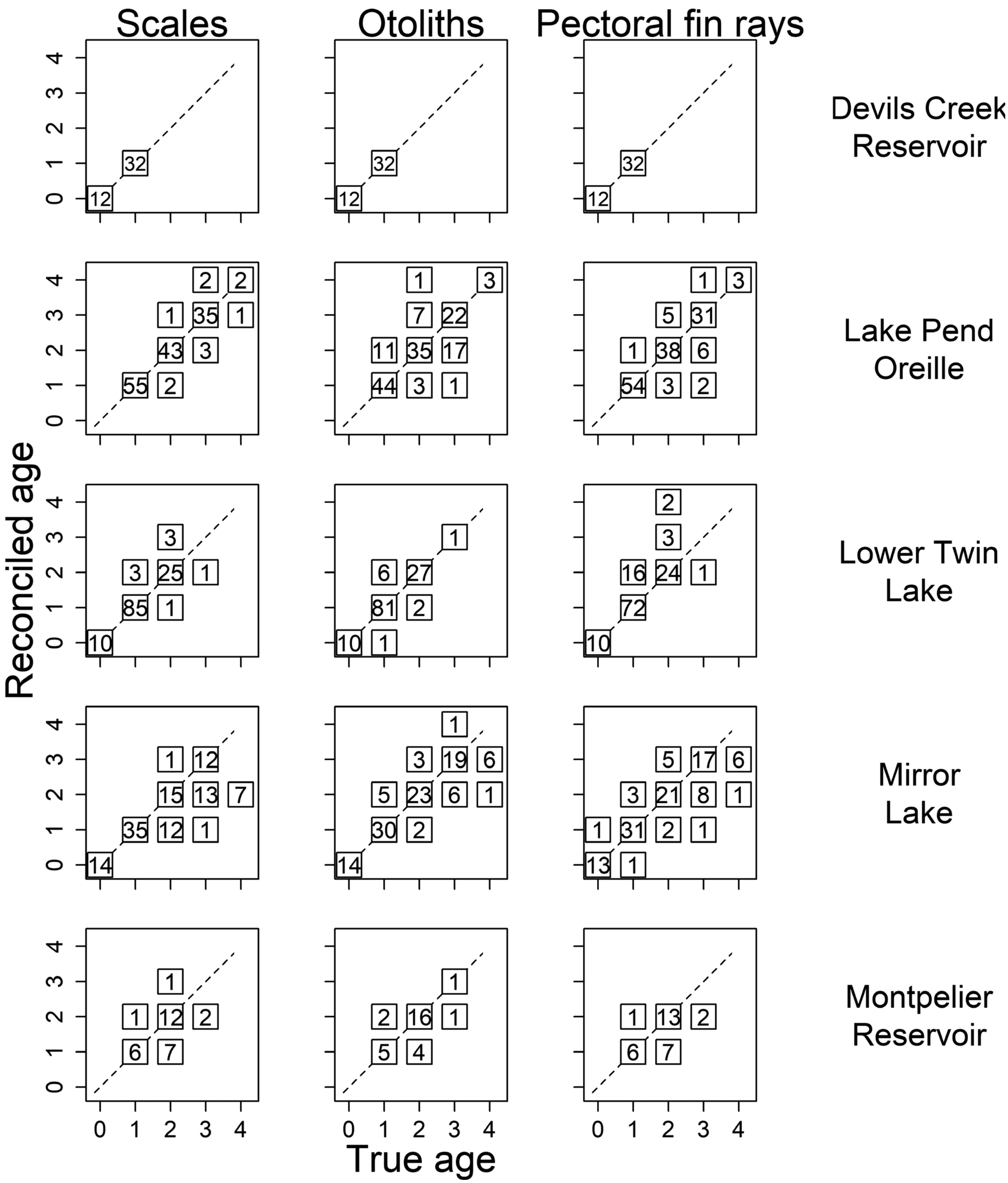

FIGURE 4. Age-bias plots comparing reconciled age estimates inferred from scales, sectioned otoliths, and sectioned pectoral fin rays to the true ages (years) of 455 kokanee sampled from five lentic water bodies across Idaho. The number in each box corresponds to the number of observations at each point and the dashed line represents exact agreement

bodies. Scales are commonly used to estimate fish ages because they are quick and inexpensive to process and do not require euthanizing the fish (Quist et al. 2012). Although scales have been used regularly to age salmonids, accuracy generally declines when assigning ages to individuals older than age 2 (Phelps et al. 2017), as

TABLE 3. Results of model selection used to evaluate the effect of water body, aging structure, and reader on the probability of estimating a correct age for 311 kokanee sampled from four lentic water bodies across Idaho (AIC_c = Akaike's information criterion corrected for small sample size; ΔAIC_c = difference in AIC_c between the given model and the top model; K = number of parameters; w_i = Akaike weight).

Model	AIC_c	ΔAIC_c	K	w_i
Water Body + Structure + Reader + (Water Body × Structure) + (Reader × Structure) + True Age	2,375.3	0.0	19	>0.99
Water Body + Structure + (Water Body × Structure) + True Age	2,425.5	50.24	13	<0.01
Structure + Reader + (Reader × Structure) + True Age	2,426.4	51.16	10	<0.01
Reader + True Age	2,437.0	61.74	4	<0.01
Water Body + True Age	2,444.3	69.09	5	<0.01
Structure + True Age	2,475.3	100.07	4	<0.01
True Age	2,488.5	113.22	2	<0.01
Intercept only	2,863.7	488.46	1	<0.01

TABLE 4. Parameter estimates and 95% confidence intervals (CIs) for all variables included in the top model (see Table 3) from a suite of candidate models that evaluated the effect of water body, aging structure, and reader on the probability of estimating a correct age for 311 kokanee sampled from four lentic water bodies across Idaho.

Parameter	Estimate	95% CI
Intercept	29.85	13.88–77.92
Mirror Lake	0.39	0.15–0.88
Montpelier Reservoir	0.22	0.08–0.53
Lower Twin Lake	0.22	0.08–0.49
Reader 2	2.16	1.45–3.24
Reader 3	1.88	1.27–2.80
Otoliths	5.71	0.93–109.79
Scales	1.46	0.40–5.97
True Age	0.39	0.34–0.44
Mirror Lake × Otoliths	0.17	0.01–1.07
Montpelier Reservoir × Otoliths	0.20	0.01–1.39
Lower Twin Lake × Otoliths	0.42	0.02–2.62
Mirror Lake × Scales	0.47	0.11–1.78
Montpelier Reservoir × Scales	0.54	0.12–2.27
Lower Twin Lake × Scales	1.22	0.29–4.64
Reader 2 × Otoliths	1.14	0.62–2.11
Reader 3 × Otoliths	1.31	0.72–2.42
Reader 2 × Scales	0.81	0.46–1.44
Reader 3 × Scales	1.59	0.88–2.88

observed in this study. Scales have been shown to outperform sectioned otoliths and pectoral fin rays for Mountain Whitefish *Prosopium williamsoni* (Watkins et al. 2015), but most studies have concluded that scales are less reliable for use in aging salmonids. For example, otoliths have provided improved (i.e., more accurate) age estimates compared to scales for Rainbow Trout (Hining et al. 2000), Columbia River Redband Trout *O. mykiss gairdneri* (Schill et al. 2010), Arctic Char *Salvelinus alpinus* (Baker and Timmons 1991), and Lake Trout (Sharp and Bernard 1988).

Overall, age estimates inferred from all hard structures in this study yielded variable agreement with true age. Copeland et al. (2007) evaluated known-age Chinook Salmon *O. tshawytscha* in Idaho and reported that fin rays were 99% accurate, whereas scales were 82% accurate. Klein et al. (2017) evaluated known-age Largemouth Bass *Micropterus salmoides* in Georgia and reported that sectioned otoliths were 92% accurate. Hining et al. (2000) recaptured 100 Rainbow Trout from two southern Appalachian streams 12–15 months after marking and reported that all 100 fish had formed an additional annulus on their otoliths. Our results demonstrate that a particular calcified structure might produce relatively accurate age estimates for one water body (i.e., one population) while simultaneously underperforming at a different water body. Erickson (1983) demonstrated that the percent agreement of sectioned otoliths, sectioned dorsal fins, and scales for estimating age of Walleyes *Sander vitreus* produced similar results at two Manitoban lakes but differed substantially at two other lakes. The authors attributed the relatively poor performance of the calcified structures to slow growth of Walleyes in those systems. To our knowledge, this study represents the first attempt to validate age estimates for kokanee; thus, we encourage additional aging studies across several populations to determine whether structures are inherently more difficult to age for kokanee than for other salmonids, perhaps due to diet, local environmental conditions (e.g., water temperature, habitat, and water chemistry), fish growth, or some other reason.

Error associated with age estimates can occur as process error, such as the absence of a true annual mark, or as interpretation error, wherein the reader is unable to match age estimates with true age (Maceina et al. 2007). Both process and interpretation errors may occur for several reasons. For example, slow growth of an individual can crowd annuli on scales, potentially resulting in inaccurate age estimates (Hoxmeier et al. 2001; Quist et al. 2012). However, Lake Pend Oreille kokanee exhibited the slowest growth during this study yet had a low error rate when scales were used to assign ages. Mirror Lake kokanee experienced growth similar to that of Lake Pend Oreille fish, but the error rate for scale age assignments was much higher, suggesting that local environmental conditions may be affecting readability of the structure. Reconciled age assignments for the fast-growing fish sampled from Devils Creek Reservoir were 100% accurate, although it is unclear whether the improvement in accuracy can be attributed to a fewer number of age-classes sampled, faster growth, or a combination of these factors. Slow growth has been attributed to poor accuracy in age estimates for Walleyes (Erickson 1983), but the average life span of Walleyes is much longer than that of kokanee. Given that aging accuracy is highest for younger fish, and 97% of the kokanee we examined were age 3 or younger, the observed discrepancies in accuracy between the current study's calcified structures and those of other studies are surprising. Disentangling the mechanism behind the relatively poor accuracy of kokanee aging structures will require further research at additional water bodies.

In addition to process error, interpretation error likely served as a source of error in this evaluation. False annuli, which can reduce aging precision (Ross et al. 2005), were frequently identified on kokanee scales, fin rays, and otoliths throughout this study. In addition, otoliths from Lake Pend Oreille and Mirror Lake were often overly opaque, making interpretation difficult—a phenomenon that has been reported previously for other salmonid species (Chilton and Bilton 1986; Copeland et al. 2007). Many otoliths examined in this study exhibited double-banding patterns or indiscrete slow- and fast-growth zonation. The banding patterns and annulus formation on the otoliths we examined appeared to be inconsistent among individual kokanee and led to disagreement among readers on annulus identification. Similarly, Hoxmeier et al. (2001) reported that Bluegills *Lepomis macrochirus* with more false and vague annuli on calcified structures had reduced accuracy and precision. Gaining familiarity with the subtleties associated with aging any particular stock of kokanee would likely improve aging accuracy and precision, as demonstrated by the scale data from Lake Pend Oreille. Nevertheless, evaluating the precision and accuracy of hard structures should be incorporated into any study to fully understand those nuances and make comprehensive and informed management decisions.

In conclusion, the variation in accuracy among calcified structures and water bodies observed in the present study suggests that local conditions (e.g., water temperature, water chemistry, and fish growth rates) likely affect the accuracy of kokanee age estimates. Given the results of age assignments coupled with population-specific growth summaries, our data suggest that accuracy and precision will be reduced for populations with lower annual growth rates. As such, we recommend that pilot evaluations be conducted for any kokanee population to determine whether annulus interpretation is more accurate when using a particular calcified structure. Furthermore, these data demonstrate the benefit of conducting age validation studies across different populations. Mounting otoliths and pectoral fin rays in epoxy and sectioning them require substantially more processing time than preparing scales (Isermann et al. 2003; Koch and Quist 2007; Vandergoot et al. 2008), so processing time should be a consideration when selecting a hard structure to age. For instances in which a pilot evaluation has not been conducted, aging more than one calcified structure may improve reconciled ages for kokanee populations.

ACKNOWLEDGMENTS

We thank B. Ament, B. Harryman, D. Daw, K. Gatt, J. Everson, K. Stevenson, J. Thiessen, R. Raymondi, S. Elle, L. Mamer, and J. Cassinelli for their assistance with collecting, processing, and aging the kokanee structures. We also appreciate C. Watkins and M. Quist for their valuable input on collecting, processing, and reading pectoral fin rays. Additional thanks are extended to C. Watkins and D. Schill for reviewing an earlier draft of the manuscript. Funding for this project was provided by anglers and boaters through their purchase of Idaho fishing licenses, tags, and permits; from federal excise taxes on fishing equipment and boat fuel through the Federal Aid in Sport Fish Restoration Program; and by the Bonneville Power Administration. There is no conflict of interest declared in this article.

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