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BRIEF COMMUNICATION

Chinook salmon *Oncorhynchus tshawytscha* (Walbaum, 1792) life history influences how diagnostic cranial structures relate to fish length

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Abstract

Diagnostic bones can aid in identification and size determination of fishes from ingested prey, archaeological remains or damaged specimens. We extracted diagnostic structures, including cleithra, dentaries, opercles and otoliths, from juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*) from three distinct groups: hatchery, naturally produced and surrogate, representing shared genetics. Although our observations highlight that growth and life history are important considerations in structuring allometry, we note that a wide variety of diagnostic bones and measurement axes may be suitable for determining body lengths where remains may be damaged or incomplete.

KEYWORDS
allometry, growth, head, length regressions, morphology, predation

Researchers can use specific bones and similar diagnostic structures and their characteristics (size, shape, density) to identify animals. When sufficiently distinct, diagnostic structures can identify fish to the species level (Parrish et al., 2006) and can greatly increase information available from archaeological and gut content studies where whole fish in measurable condition may be rare or non-existent (Erhardt et al., 2018; Mannermaa, 2016; Miller et al., 2011; Sanchez, 2020). Common diagnostic bones used to identify juvenile salmonids include the dentary, cleithrum and opercle, in addition to otolith structures (hereafter referred to as 'bones') of the head (Hansel et al., 1988; Parrish et al., 2006). Depending on the fish species and available data, diagnostic bones can provide highly accurate identification and estimates of body length (Hansel et al., 1988; Parrish et al., 2006), though care is needed to ensure comparability across studies. Information derived from diagnostic skeletal remains can be used to examine historical fish populations to approximate growth using estimated fish sizes, to identify predator diets, including fish remains for prey availability, preference and potential gape limitations, and to track changes in size and composition metrics over time (Erhardt et al., 2018; Sanchez, 2020). Linear regressions on measurements of these commonly used diagnostic bones can represent an almost perfect match between bone length and body length, with coefficients of determination up to 0.99 (Hansel et al., 1988). However, fish may exist in mixed stocks which grow at different rates. Although the influence of differential rearing and growth experiences on external morphology is well documented for some species (Cogliati et al., 2010), it remains unclear what implications this might have for bone-to-length regressions. Data for some species, especially at the levels of populations and across life stages, can be limiting or contradictory due, in part, to inconsistencies in species identification, even by experts (Gobalet, 2001), and because growth rate variation may result in changes to allometric relationships (Casselman, 1990). These issues highlight the potential importance of accurate identification of the species, size, location and date of fish sampling and are particularly important where diagnostic bones may provide invaluable information on ontogeny, population size metrics and predation for species of concern.

Here, we explore measurements on diagnostic bones for juvenile Chinook salmon *Oncorhynchus tshawytscha* (Walbaum, 1792), a

species listed as threatened or endangered through much of its native range (Ford et al., 2011; Myers et al., 1998) and for which diagnostic bone measurements relative to body size appear inconsistent across distinct populations and life histories, meaning that no universal measurements exist. We compile literature values for previous regressions developed for spring versus fall run juveniles and compare these to newly collected data. To further investigate the role that rearing methods could play in bone-to-length relationships, we examined specimens from three groups with shared genetics from the Willamette River basin, Oregon: conventionally reared hatchery spring Chinook salmon ('hatchery'), naturally produced spring Chinook salmon collected as mortalities below a dam ('naturally produced') and surrogate spring Chinook salmon ('surrogate') reared to mimic the morphology and growth trajectory of naturally produced juveniles. The external meristic differences of the three groups examined here have been well documented (Billman et al., 2014). However, it is unknown whether those differences result in significant differences in diagnostic bone-to-length relationships, and what variability in measurements could result from the application of regressions developed where different life histories and associated growth trajectories overlap. For example, we expected that the unique head shape of traditional hatchery-raised juveniles could impact the comparisons of bone length-to-fish length regressions relative to surrogate- and natural-origin fish (Cogliati et al., 2019). Using known-length individuals to create reference datasets, we clarify how our measurement axes differ from prior studies and present comparisons of regression slopes and model fits for characterizing body lengths from bone lengths.

All fish sampled represent spring Chinook salmon from the Willamette River basin and were expected to represent a single genetic pool (Johnson & Friesen, 2014). The Willamette River is a tributary of the Columbia River, joining at the confluence near Portland, Oregon. Fish for this study were collected in 2013 and 2022. For the 'hatchery' fish, staff from the Oregon Department of Fish and Wildlife (ODFW) collected juvenile spring Chinook salmon (47–106 mm fork length) in 2013 from Leaburg ($n = 30$) and McKenzie fish hatcheries ($n = 10$) in the upper Willamette River basin, Oregon. Fork lengths (mm) of individual fish were measured before freezing. Both hatcheries are managed together, representing a single stock originating from wild upper Willamette spring Chinook salmon from the McKenzie River, and regularly include naturally produced broodstock along with returning hatchery fish (Oregon and Department of Fish and Wildlife, 2022). In 2022, McKenzie River stock 'surrogate' fish were periodically collected by ODFW staff from the Fish Performance and Genetics Laboratory at Oregon State University in Corvallis, Oregon. Although genetically comparable, surrogates were raised using conditions and diet designed to produce a juvenile with growth trajectories and morphometric characteristics as similar as possible to naturally produced juveniles in the region (Cogliati et al., 2019).

Fish were collected in accordance with the Guide for the Care and Use of Laboratory Animals and state and federal permits, including Oregon State University Institutional Animal Care and Use Permit IACUC-2021-0154 and NOAA 4d Scientific Take Permits 17457, 24296, 26221 and 26276. Hatchery and surrogate fish were euthanized using a Tricaine methane sulfonate (MS-222) bath at concentration >250 mg/L buffered with sodium bicarbonate to pH of 6.5–7.5. All fish were measured in fork length (mm) and weighed (g) before freezing and subsequent processing. We were not able to administer additional physical methods (e.g., blunt force to the cranium) following immersion because our study relied on recovery of intact cranial structures for identification. 'Naturally produced' fish, the result of natural spawning and rearing in the South Fork McKenzie River, were collected by Environmental Assessment Services staff as passively collected mortalities in a rotary screw trap deployed below Cougar Dam on the South Fork McKenzie River in 2022.

Fish were individually bagged and tagged with a unique ID, date and place of collection, and kept frozen until processed. Fork lengths were confirmed in the laboratory before heads were removed and placed in individual sealed bags. Bones were extracted by submerging watertight bags in a constant temperature bath of 49°C water for 24 h. Flesh was then removed with a toothbrush or small paintbrush. Bones with remaining tissue were soaked in 3% hydrogen peroxide for 48 h, brushed again until clean and placed into vials filled with 95% ethanol.

We used a microscope digital camera and software (e.g., AmScope MU300 3MP or MU1000 10MP) to measure diagnostic bones, calibrating measurements with an ocular micrometre. Each bone was measured to the nearest micrometre as follows (Figure 1): the inner face (sulcus side up) of left otolith was measured for otolith length, from the posterior end to anterior end (usually extending to the tip of the ostium in Chinook salmon). The lateral side of left cleithrum was measured for horizontal limb length, from the ventral tip to the exterior of the dorsal posterior lobe. The lateral side of left dentary was measured for dentary body length (ventral length), from the symphyseal margin to the posterior end of the ventral leg. The medial side of left opercle was measured for opercle height, the vertical measurement of the bottom to the top of the anterior margin.

To compare the effect of group (hatchery, naturally produced, surrogate) on the regression slopes for data collected in the present study, we used the analysis of covariance (ANCOVA) implemented in R Statistical Computing and Shapiro–Wilk test of normality on residuals (R. Core Team, 2014). We log transformed fork length in relation to opercle height to achieve normality. Figures were generated using ggplot2 (Wickham, 2016). We used the differences in slopes to identify bones that were the most responsive to changes in fish length (bones that changed rapidly with fish size) and adjusted R^2 to assess the variability or consistency of the relationship between a given measurement axis and fish length.

We also used examples from the literature of comparable bone measurements for juvenile Chinook salmon from spring and fall migratory ecotypes, including the Pacific Coast broadly, British Columbia, the Snake River basin and California's Central Valley, and regressions with fork length (Table 1). Units were converted to millimetre as necessary, and WebPlotDigitizer (Rohatgi, 2017) was used to determine the slope and intercepts of linear regressions from plots when tables were not included in the literature.

Diagnostic bone measurements were typically highly correlated with fish length (mean adjusted R^2: 0.90 ± 0.08; Figure 1; Table 1).

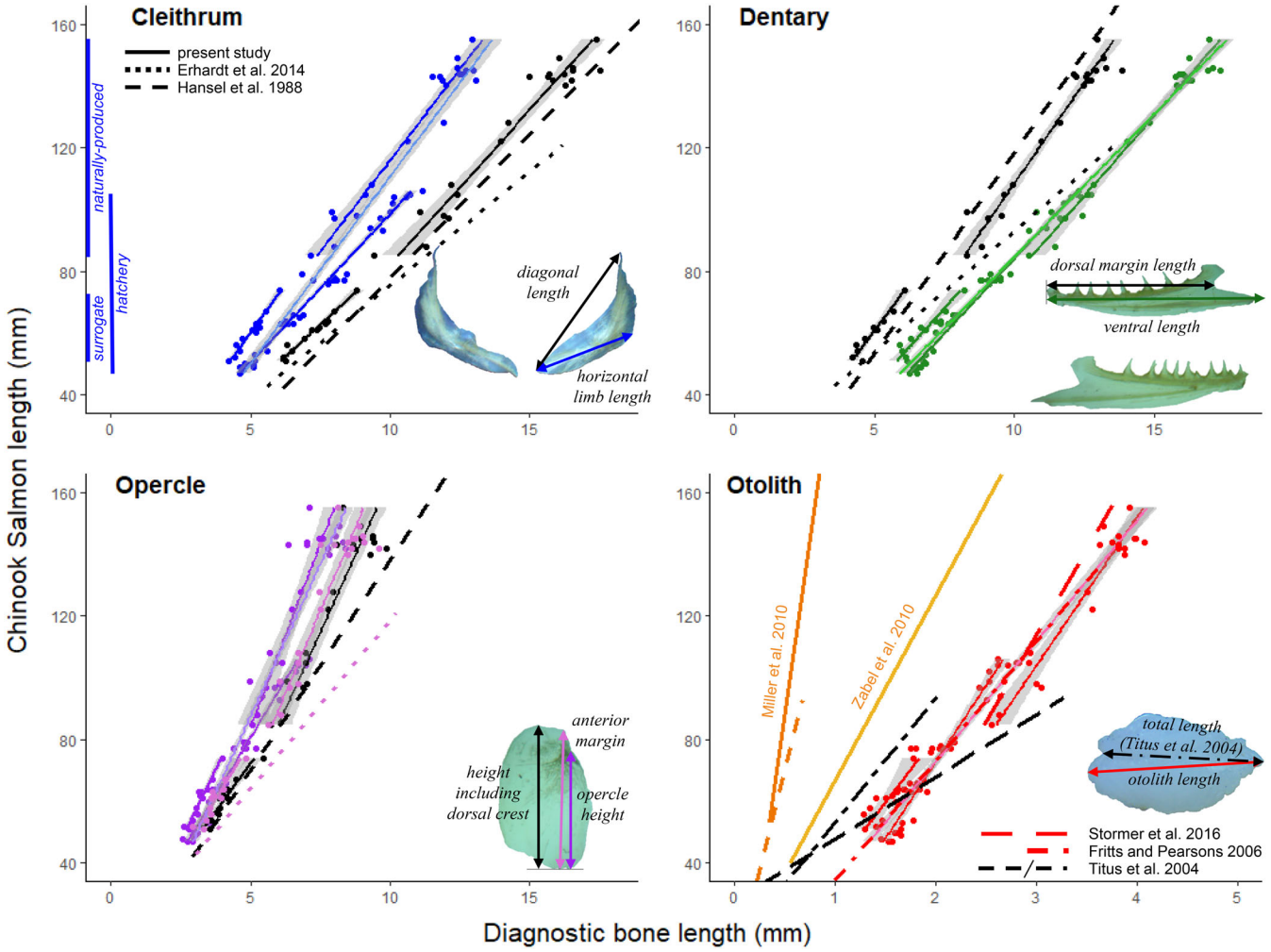

FIGURE 1 Juvenile spring Chinook salmon *Oncorhynchus tshawytscha* diagnostic bones and measurements from the present study (solid line regressions and associated colour-coded points) for surrogate, hatchery and naturally produced groups (size ranges indicated on *y*-axis of the upper left panel), as well as associated composite regressions (paler solid lines) and 95% confidence intervals (shading), plotted with regressions from Hansel et al. (1988) (dashed line) and Erhardt et al. (2014) (dotted line) for cleithrum, dentary and opercle bones. Otolith measurements are plotted with Stormer et al. (2016) (long dash red line), Fritts and Pearsons (2006) (dash dot red line) and Titus et al. (2004) (dashed and dotted black lines for Lower American River and Nimbus Hatchery, respectively). Diagnostic bones are pictured along with the comparable measurement axes for each of these studies (arrows of corresponding colours and styles). Measurement axes for regressions from Zabel et al. (2010) of otolith radius for fall (solid orange) and spring (dashed orange) Chinook salmon, as well as Miller et al. 2010 regressions for otolith width (solid goldenrod), are not pictured on the example structure photograph. Otolith *x*-axis scale differs from other panels to better illustrate measurements corresponding to its smaller structure. Each regression line is limited to the range of fish lengths used in its respective calculation (see Table 1).

The longest bone measurements were obtained from dentary bones followed by cleithrum, opercle and otolith (Table S1). Bone measurement lengths generally corresponded to the expected change in fish length (as mm FL) per millimetre change in bone measurement, though the cleithrum diagonal length had the greatest change per millimetre for each millimetre change in fish fork length (1 mm bone: 8.1–9.4 mm fish), slightly greater than the change for dentary bone ventral length (1 mm bone: 9.1–9.9 mm fish; Figure S1). Opercle height was intermediate in its length relationship to fish length (1 mm bone: 14.4–18.4 mm fish) and otolith length had the least increase in bone length per millimetre for each millimetre increase in fish size (1 mm: 29.7–45.4 mm fish). As expected, when measurements for all groups were available, the mixed-origin model produced values intermediate to these ranges (Table 1). Overall, measurements were similar in their ability to predict fish fork length and were comparable to the predicted fit values reported for alternate measurements of the cleithrum, dentary and opercle bones by Hansel et al. (1988; R^2 values of 0.98).

For data collected in this study from genetically comparable fish, life history in the form of hatchery, surrogate or naturally produced groups had a significant interactive effect with diagnostic bone length for cleithrum and dentary bones, indicating slopes were significantly different based on group (Table S2). This may be consistent with differential growth as, excluding otoliths, our regressions were most different from those reported by Erhardt et al. (2014) for juvenile fall Chinook salmon from the Snake River (the largest tributary of the

TABLE 1 Representative measurement axes (as shown in Figure 1) for Chinook salmon *Oncorhynchus tshawytscha* diagnostic bones with corresponding linear regression and fit metrics for this and historical studies in the form [fork length (mm) = intercept + slope × bone measurement (mm)].

Bone	Axis	Intercept	Slope	Fit (R^2)	Fork length range (mm)	*n*	Location/run (spring or fall)	Reference
Cleithrum	Horizontal limb length	4.232	9.385	0.975	47–106	40	Leaburg and McKenzie River hatcheries/ spring Chinook	Present study
Cleithrum	Horizontal limb length	4.741	11.186	0.946	85–155	21	Cougar Reservoir/spring Chinook	Present study
Cleithrum	Horizontal limb length	−0.460	12.108	0.958	51–74	12	Fish Performance and Genetics Laboratory – Smith Farm/surrogate spring Chinook	Present study
Cleithrum	**Horizontal limb length**	**−4.25**	**11.358**	**0.937**	**47–155**	**73**	**Mixed-origin Willamette River stock spring Chinook**	**Present study**
Cleithrum	Diagonal length	−9.187	9.416	0.939	85–155	21	Cougar Reservoir/spring Chinook	Present study
Cleithrum	Diagonal length	2.226	8.059	0.965	51–74	12	Fish Performance and Genetics Laboratory – Smith Farm/surrogate spring Chinook	Present study
Cleithrum	Diagonal length	−15.710	9.360	0.98	42–184	53	John Day Reservoir or hatcheries/spring Chinook	Hansel et al. (1988)
Cleithrum	Diagonal length	1.983	7.347	0.96	43–121	31	Snake River/fall Chinook	Erhardt et al. (2014)
Dentary	Ventral length	−10.995	9.497	0.981	47–106	40	Leaburg and McKenzie River hatcheries/ spring Chinook	Present study
Dentary	Ventral length	−18.839	9.937	0.953	85–155	21	Cougar Reservoir/spring Chinook	Present study
Dentary	Ventral length	−0.705	9.063	0.889	51–74	12[b]	Fish Performance and Genetics Laboratory – Smith Farm/surrogate spring Chinook	Present study
Dentary	**Ventral length**	**−6.01**	**9.081**	**0.983**	**47–155**	**72**	**Mixed-origin Willamette River stock spring Chinook**	**Present study**
Dentary	Dorsal margin length	−14.145	12.363	0.944	85–155	21	Cougar Reservoir/spring Chinook	Present study
Dentary	Dorsal margin length	4.379	11.270	0.914	51–74	12[b]	Fish Performance and Genetics Laboratory – Smith Farm/surrogate spring Chinook	Present study
Dentary	Dorsal margin length	−12.110	13.050	0.98	42–184	53	John Day Reservoir or hatcheries/spring Chinook	Hansel et al. (1988)
Dentary	Dorsal margin length	14.823	7.819	0.83	43–121	30	Snake River/fall Chinook	Erhardt et al. (2014)
Opercle	Opercle height	8.479	14.411	0.964	47–106	40[c]	Leaburg and McKenzie River hatcheries/ spring Chinook	Present study
Opercle	Opercle height	1.799	18.387	0.763	85–155	21	Cougar Reservoir/spring Chinook	Present study
Opercle	Opercle height	5.097	17.182	0.924	51–74	12	Fish Performance and Genetics Laboratory – Smith Farm/surrogate spring Chinook	Present study
Opercle	**Opercle height**	**−3.074**	**18.138**	**0.918**	**47–155**	**72**	**Mixed origin Willamette River stock spring Chinook**	**Present study**
Opercle	Opercle height, including dorsal crest	−9.680	16.881	0.840	85–155	21	Cougar Reservoir/spring Chinook	Present study
Opercle	Opercle height, including dorsal crest	15.728	11.050	0.875	51–74	12	Fish Performance and Genetics Laboratory – Smith Farm/surrogate spring Chinook	Present study
Opercle	Opercle height, including dorsal crest	2.340	13.560	0.98	42–184	53	John Day Reservoir or hatcheries/spring Chinook	Hansel et al. (1988)

TABLE 1 (Continued)

Bone	Axis	Intercept	Slope	Fit (R^2)	Fork length range (mm)	*n*	Location/run (spring or fall)	Reference
Opercle	Anterior margin	−13.101	18.110	0.834	85–155	21	Cougar Reservoir/spring Chinook	Present study
Opercle	Anterior margin	13.026	12.689	0.846	51–74	12	Fish Performance and Genetics Laboratory – Smith Farm/surrogate spring Chinook	Present study
Opercle	Anterior margin	9.844	10.888	0.89	43–121	12	Snake River/fall Chinook	Erhardt et al. (2014)
Otolith	Length	−17.746	45.377	0.915	47–106	40	Leaburg and McKenzie River hatcheries/ spring Chinook	Present study
Otolith	Length	−25.682	43.930	0.913	85–155	21	Cougar Reservoir/spring Chinook	Present study
Otolith	Length	15.505	29.660	0.666	51–74	12	Fish Performance and Genetics Laboratory – Smith Farm/surrogate spring Chinook	Present study
Otolith	**Length**	**−1.137**	**37.362**	**0.956**	**47–155**	**73**	**Mixed-origin Willamette River stock spring Chinook**	**Present study**
Otolith	Length	−54.445	56.131	0.71	85–156	70	Nanaimo R. hatchery/ocean-type Chinook (≈ fall Chinook)	Stormer et al. (2016)
Otolith	Length	−4.6229	38.913	0.93	30–138	30	Yakima River/predominantly fall Chinook	Fritts and Pearsons (2006)
Otolith	Total otolith length	−1.410	50[a]	0.82	32.7–93.6	36	Lower American River/fall Chinook	Titus et al. (2004)
Otolith	Total otolith length	13.400	40[a]	0.91	32.4–94.7	55	Nimbus Hatchery/fall Chinook	Titus et al. (2004)
Otolith	Radius	−26.540	230[a]	0.857	53–168	61	Snake River/fall Chinook	Zabel et al. (2010)
Otolith	Radius	5.060	130[a]	0.817	34–93	296	Snake River/spring–summer Chinook	Zabel et al. (2010)
Otolith	Width	6.910	60[a]	0.93	40–166	123	Mixed locations/fall Chinook	Miller, Gray, and Merz (2010)

Note: Fit for current study is presented as adjusted R^2. The three groups in the present study represent shared genetics but unique rearing conditions. Bold indicates linear regressions using data for all three groups.

[a]Converted from μm.

[b]One fish had unrecovered dentary bones and was not measured.

[c]One fish had damaged opercles and was not measured.

Columbia River). Although fit was high for individual and mixed group models, different datasets consistently produced models specific to their sample population, even for bones with nearly identical linear model slopes. A 10-mm cleithrum diagonal length, for example, could be calculated as a 75-mm (Erhardt et al., 2014) to 85-mm (naturally produced, present study) juvenile. Our results across groups were more similar to the corresponding literature measurements for juvenile spring Chinook salmon in Hansel et al. (1988) (Figure 1).

Although measurement axis was important to determining diagnostic bone-to-length relationships (as indicated by colour groups in Figure 1), considering our paired measurement axes collected on the cleithrum, dentary and opercle bones for the naturally produced and surrogate groups, models fit to the different axes were comparable in fit, differing by at most 0.02 adj. R^2 for axes measured on the same diagnostic bone (Table 1).

The similarity in model fit across different bones and their respective measurements offers a large toolset for estimating juvenile spring Chinook salmon fork length from limited or damaged skeletal remains. This is important, as diet or archaeological remains may be incomplete and not all bones may be undamaged. Additionally, it was previously unknown whether external meristic differences such as those documented in this system, where different life histories and associated growth trajectories overlap and may not be distinguished by limited remains, would result in meaningful differences in diagnostic bone-to-length relationships (Billman et al., 2014). Understanding both the ideal measurements and the impact of different life histories on diagnostic bones may be important to management where the ability to accurately estimate juvenile Chinook salmon fork length may be particularly useful in evaluating size-dependent predation risk and consumption (see Fritts & Pearsons, 2006 and Erhardt et al., 2018 as

examples). Previous research suggests that even easily digestible Chinook salmon fry may be reasonably represented in stomach content samples (Murphy et al., 2021).

Cleithrum and dentary bones had the greatest change in length with fork length and the strongest correlations, suggesting a possible role of measurement error. The larger relative size of these bones may provide a buffer against inaccuracies due to rounding (to the nearest micrometre or millimetre) that appears common in this and other studies. It could also make these measurements less sensitive to digestion (Butler & Schroeder, 1998) if bones erode at similar rates. Although relationships might suggest these are ideal bones for fork length calculations, they were also the bones that had significantly different slopes for our hatchery, surrogate and naturally produced groups. This may indicate that other structures are preferred where multiple life histories or growth trajectories overlap within the same area, as in the case of the Willamette River basin. Although some over or underestimation might be expected across groups, the importance of these differences will depend on the use of the data, and errors in studies may exist even in empirically measured fish lengths (Bunch et al., 2013). As remains may make origin impossible to distinguish, researchers may wish to consider whether a universal regression is sufficient. In this case, universal regressions using all three origins were comparable in fit to origin-specific regressions consistent with the associated increase in sample size.

Likely because of its more limited change in fish length, otolith length led to greater differences in fish fork length estimates than the other measurements assessed here. The alternate regression slopes for the same axis measurement in this study versus historical studies could also be attributable to population-level differences, as otolith shape has been shown to vary with genetics and life history (Koeberle et al., 2020). Interestingly, although otolith width may be a better predictor of juvenile salmon length than otolith length (Miller, Gray, & Merz, 2010), and logarithmic relationships between otolith width and length for Chinook salmon may be more appropriate over larger size ranges (Harvey et al., 2000), the small changes in otolith width with respect to fish length could make these measurements more susceptible to error. For our study, logarithmic regression of otolith versus size measurements did not markedly improve model fit versus linear regression for any of the fish groups (adj. R^2 difference <0.1). Water temperature, water chemistry and changes in food availability may also alter otolith morphology seasonally for similar-sized juveniles (Stormer et al., 2016; Wexler et al., 2023). Although using alternate bone measurements or a combination of structures for comparison may be preferable to otoliths alone, otoliths were the most commonly measured bone in the literature and included additional uses in ageing and saltwater entry analyses (Miller, Wells, et al., 2010).

Our study relied on two-dimensional (2D) measurements of bones, which has been shown to be not comparable to 3D computed tomography (CT)-generated models of morphometrics, as 2D does not capture lateral body depth (Buser et al., 2018). However, as with the bones selected for ease of species identification, using 2D measurements to determine length relationships presents a more practical solution for studies that may lack equipment, expertise and other resources for full CT modelling of partially digested remains. Preservation may also play a role in the accuracy of regressions. Here, fish were measured before freezing and processing. Erhardt et al. (2014), for example, used measurements from fish preserved in ethanol, which could be expected to reduce body lengths. However, similar preservation methods in sockeye salmon juveniles found ethanol preservation changed fork length by <2% (Shields & Carlson, 1996), a number that is substantially less than the differences in predicted lengths across groups and studies here.

Comparing our data and that of Hansel et al. (1988) on spring Chinook salmon to data from Erhardt et al. (2014) on fall Chinook salmon, it appears that spring and fall Chinook salmon regressions may be particularly incomparable. For example, using our bone lengths corresponding to a 121-mm spring Chinook salmon and comparing to the Erhardt et al., 2014 regression for fall Chinook salmon would result in up to an 18% difference in predicted fork length estimates for a cleithrum diagonal length of 16.2 mm, up to a 36% difference in predicted fork length estimates for a dentary dorsal margin length of 13.6 mm and up to a 41% difference in predicted fork length estimates for an opercle anterior margin length of 10.2 mm. This could be either due to population-specific differences or due to the influence of growth rate on allometric relationships between bone structures and fish length (Casselman, 1990). Differences in head shape are plausible drivers, as previous studies using morphometrics have found that Chinook salmon head morphology has been shown to relate to smolting (Beeman et al., 1994) and hatchery origin (Tiffan & Connor, 2011). Tiffan et al. (2000) found Chinook salmon head size corresponded to age, but that body morphology could not accurately predict fall versus spring runs, though run type was associated with the greatest differences in bone allometry observed here, even comparing hatchery and naturally produced spring Chinook salmon to the potentially mixed run represented by Erhardt et al. (2014).

Considering the cultural and ecological importance of Chinook salmon (Lichatowich, 2001), improving our ability to understand current and historical trends in their ontogeny, predation, mortality and length will be important to conservation efforts. The incorporation of size estimates in piscivore diet and historical midden data can improve our long-term understanding of fish population and community dynamics. Ensuring that similar regressions exist for other fishes could improve our ability to use skeletal remains to further assess predation and community patterns. Improvement in modern data capture, digital imaging and measurements could allow for rapid processing and identification of likely distinct remains in bulk, reducing costs associated with individual measurements (Arismendi et al., 2021). These advances could increase data availability and application of diagnostic bones to better understand population and community dynamics. Based on our results, any of a wide variety of diagnostic bones and their measurements may prove suitable for determining fish lengths with relatively high accuracy, providing diagnostic relationships and increased flexibility for future studies. However, caution should be used in ensuring consistent measurement axes and comparable populations so that regressions are applicable to the fish being modelled.

AUTHOR CONTRIBUTIONS

Jeremy D. Romer: conceptualization, data curation, funding acquisition, investigation, methodology and writing – original draft. Kevin A. Stertz: conceptualization, data curation, investigation and writing – review and editing. Keiara Pham: investigation and writing – review and editing. Christina A. Murphy: formal analysis, resources, visualization and writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no competing interests.

DATA AVAILABILITY STATEMENT

All data underlying this article are available within the article and associated Supporting Information. Questions about data can be directed to Jeremy D. Romer (jeremy.d.romer@odfw.oregon.gov).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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