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Genetics of century-old fish scales reveal population patterns of decline

Michael H.H. Price MSc[1] | Brendan M. Connors PhD[1,2] | John R. Candy MBA[3] | Brenda McIntosh BSc[3] | Terry D. Beacham PhD[3] | Jonathan W. Moore PhD[1] | John D. Reynolds PhD[1]

[1]Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

[2]Fisheries and Oceans Canada, Institute of Oceans Sciences, Sidney, BC V8L 5T5, Canada

[3]Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC V9T 6N7, Canada

Correspondence
M. H. H. Price, Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.
Email: mhprice@sfu.ca

Abstract

Conservation scientists rarely have the information required to understand changes in abundance over more than a few decades, even for important species like Pacific salmon. Such lack of historical information can underestimate the magnitude of decline for depressed populations. We applied genetic tools to a unique collection of 100-year-old salmon scales to reveal declines of 56%–99% in wild sockeye populations across Canada's second largest salmon watershed, the Skeena River. These analyses reveal century-long declines that are much greater than those based on modern era abundance data, which suggested that only 7 of 13 populations declined over the last five decades. Populations of larger-bodied fish have declined the most in abundance, likely because of size-selective commercial fisheries. Our findings illustrate how a deep historical perspective can expand our understanding of past abundances to a time before species incurred significant losses from fishing, and help inform conservation for diminished populations.

KEYWORDS

conservation genetics, ecosystems, fisheries, historical ecology, population depletion, recovery, salmon, extinction risk, Skeena River

1 | INTRODUCTION

Declines in population abundance of many of Earth's biota are outpacing species extinctions (Hughes, Daily, & Ehrlich, 1997), and disrupting ecosystems and human cultures. For example, loss of bison (*Bison bison*) populations decimated a cultural foundation of Indigenous peoples, and fundamentally re-shaped grasslands (Gaston & Fuller, 2008). Yet managers rarely have the historical information required to assess changes in abundance over more than a few decades, even for common species (Bonebrake, Christensen, Boggs, & Ehrlich,

2010). The absence of such historical data can lead to a shifting baseline syndrome (sensu, Pauly, 1995), whereby abundances in recent decades are incorrectly assumed to be the appropriate baselines against which to quantify trends, and assess current status. This can impair the characterization of risk, hide a legacy of stressors, and delay conservation action (Soga & Gaston, 2018).

Pacific salmon (*Oncorhynchus* spp.) are abundant species that underpin fisheries, cultures, and ecosystems around the North Pacific (Schindler et al., 2010). Salmon can exhibit large fluctuations in abundance, which at times are

synchronous across broad regions due to large-scale climatic processes (Mantua, Hare, Zhang, Wallace, & Francis, 1997). Within each species, there are hundreds of unique, locally adapted populations; this diversity supports resilient fisheries and economies, as well as wildlife that feed heavily on salmon, such as bears (Schindler et al., 2013). However, many salmon populations have declined due to over-exploitation and habitat degradation. Over 500 populations—predominantly in their southern range—have become extinct, with Chinook (*O. tshawytscha*) and sockeye (*O. nerka*) having experienced the highest proportional losses (Gustafson et al., 2007; Slaney, Hyatt, Northcote, & Fielden, 1996).

It has proven challenging to reconstruct population-specific abundances of salmon beyond the last several decades. For instance, data that contribute to extinction-risk evaluations for sockeye in Canada routinely begin after 1950 (COSEWIC, 2017), more than 70 years after the onset of commercial exploitation. While lake sediments have provided valuable insight into population dynamics over hundreds of years (e.g., Rogers et al., 2013), such paleolimnological tools are limited to systems where marine-derived nutrients drive primary productivity or nutrient budgets (Hobbs & Wolfe, 2007). Thus, there remains a need to quantify salmon abundances at a time when commercial fisheries began, which can be used by managers to measure the magnitude of population change in species like sockeye, which have long supported commercial fisheries.

We sought to characterize changes in abundance of sockeye populations in Canada over a century spanning the onset of industrial fishing to the present, and to test four leading hypotheses to explain the patterns observed: (1) fisheries selectivity, (2) habitat degradation, (3) population productivity, and (4) freshwater migration challenges. Here we combine modern genetic tools with century-old fish tissues to uncover declines of 56%–99% in wild sockeye populations from Canada's second largest salmon system, the Skeena River; had we used existing data (i.e., from the 1960s), only 7 of 13 populations show a decline. Fisheries selectivity of larger-bodied populations is the most probable driver of differences between populations. Our deep historical perspective can help inform status assessments and rebuilding discussions for diminished populations of this iconic species.

2 | METHODS

The Skeena watershed is composed of 31 sockeye Conservation Units (CU; Holtby & Ciruna, 2007), which generally are grouped into 13 population complexes (Figure 1). An industrial fishery for these fish began at the mouth of the Skeena in 1877, and a scale-collection program commenced in 1912 (Supporting Information [SI], section A). We sampled scales from 50 fish from the collection for each of 9 fishing weeks
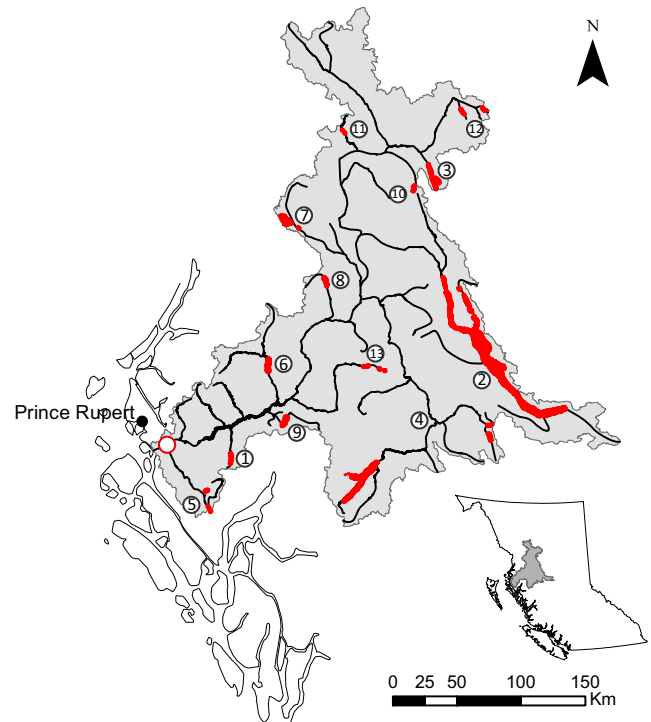

FIGURE 1 Skeena River watershed showing the location of each sockeye salmon population complex (numbers 1–13) identified in genetic analyses, and associated nursery lakes in red. White-filled red circle denotes the approximate location of historical scale sample collection, and current Skeena Tyee Test Fishery

from years 1913, 1916, and 1918–1923, for a total of 3,400 scales. We digitally photographed one scale from each fish, and aged each scale by annuli counts. DNA was extracted from scales, genotyped at up to 12 microsatellite loci, and individuals assigned to population via genetic stock identification; here, *population* refers to one or more CUs that are genetically similar to each other, yet distinct from other CUs (Beacham, Cox-Rogers, MacConnachie, McIntosh, & Wallace, 2014; SI, section B).

We reconstructed aggregate (all populations combined) total abundance (i.e., catch + spawning fish, which throughout we refer to as *abundance*) for Skeena sockeye during the entire history (1877–2018) of commercial fishing using three data sources: (1) reconstructed catch from canneries (Argue & Shepard, 2005) and exploitation derived from instantaneous fishing rates applied to the number of boats operating in each year (which varied annually; Shepard & Withler, 1958), and combine to provide total abundance (i.e., abundance = catch/exploitation rate) during 1877–1950, (2) total abundance during 1951–1969 from Wood (2008), and (3) total abundance (separated into "combined" abundance that includes production from three spawning channels at Babine Lake plus wild abundance, and "wild only" abundance)
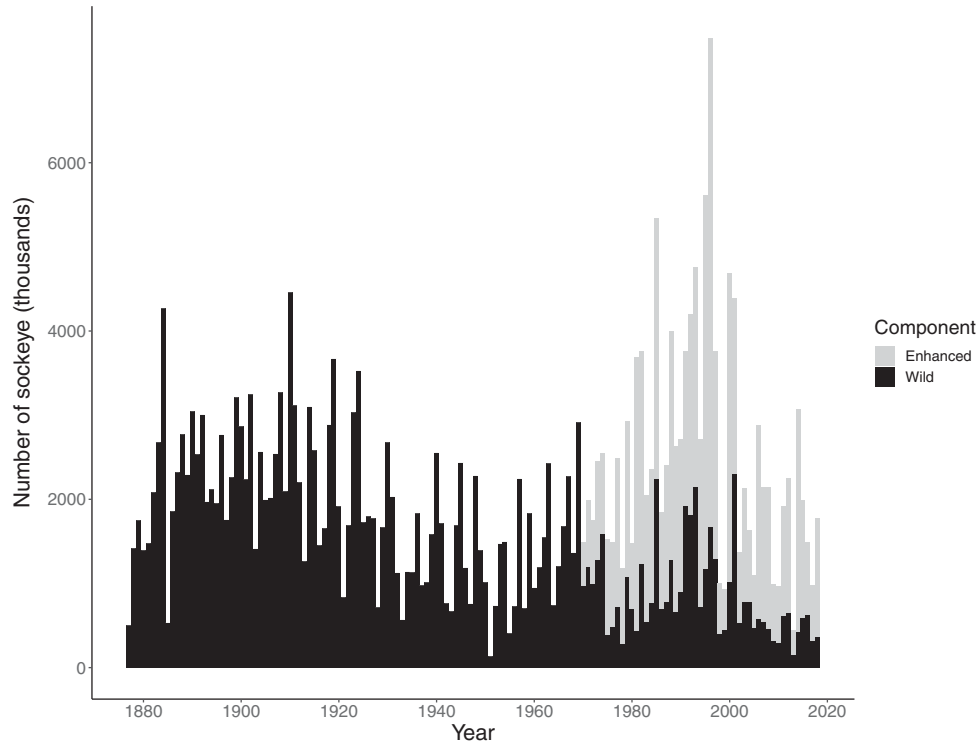
FIGURE 2 Total abundance of sockeye salmon returning to the Skeena River watershed since the beginning of commercial fishing in 1877 to 2018. Black = wild only component; gray = enhanced production from spawning channels in Babine Lake since 1970

during 1970–2018 (Cox-Rogers & Spilsted, 2012; Rosenberger & Cox-Rogers, 2019; Figure 2).

We then reconstructed annual historical (1913–1923) abundance of sockeye at the population level in a four-step process: (1) We multiplied aggregate annual abundance detailed above by the proportion of Skeena-origin sockeye genetically identified from historical scales. (2) We multiplied annual abundance (Step 1) by weekly abundance proportions—randomly drawn from one of seven (2011–2017) years of data estimated at the Skeena Tyee Test Fishery. (3) We multiplied weekly abundance estimates (Step 2) by the proportions of individual Skeena-origin populations in those fishing weeks, then summed across weeks for each population. (4) We repeated steps 2–3 50,000 times to derive a median abundance estimate for each population for each historical year (SI, section C). These run-reconstructions are based on two assumptions: (1) migration-timing of sockeye has not changed from the historical period to present, and (2) populations were equally susceptible to capture by gill-net. We examined the sensitivity of our analysis to these assumptions by shifting weekly proportions of fish one week earlier (SI, section D), and applying gill-net selectivity corrections on population abundance estimates (and body-size and age; SI, section E) to account for this in our hypothesis tests below.

To estimate the magnitude of change in abundance of populations between historical (1913–1923) and recent (2007–2014) periods, we fit a linear mixed-effects model to the

population-specific abundances with a categorical predictor variable—time-period. Annual median historical abundance estimates (corrected for gill-net selectivity) were derived from our run-reconstructions, and recent estimates are reported in English, Peacock, Challenger, and Mochizuki (2016) and SI, section F. Each model, representing a hypothesis, included an interaction term with time-period to assess how well the model explains variation in the change in abundance among populations between time-periods. We normalized our response variable (abundance) for each population by dividing each historical and recent year's abundance estimate by the average historical abundance for the population, so that all "observations" across populations are comparable.

We considered four hypotheses to explain changes in population abundance over time; specifically, we hypothesized that larger declines in abundance have occurred for populations that: (1) had larger body sizes because gill-nets catch larger-sized fish, (2) are from more degraded habitat because of lost carrying capacity, (3) had older ages because late-maturing populations tend to have lower productivity, and (4) had longer migrations because long-distance migrants face more in-river fisheries and changing hydrologic patterns. We compiled data to test our hypotheses: (1) average selectivity-corrected historical body-size (Size) as a proxy for fisheries selectivity, (2) human footprint (Footprint) as a measure of habitat degradation, (3) average selectivity-corrected historical age-at-maturity (Age) as a measure of productivity,

and (4) freshwater migration distance (Distance) as a measure of the degree to which the migration is challenging (SI, section G). We used body-size and age data from populations (scales) with ≥ 90% genetic assignment probability. We standardized each covariate by subtracting the mean and dividing by its standard deviation (SD) to compare effect sizes directly; no variable was strongly correlated with another (i.e., correlation coefficient > .5; SI, section H). Finally, we included "population" as a random effect on the intercept in each model to account for nonindependence of observations within populations at the scale that the independent variables were measured.

We fit models describing each hypothesis to the data in a Bayesian framework. We used uniform priors (i.e., all parameter values are equally likely) for each model. We fit each model with a lognormal error distribution using four chains, each with 4,000 iterations (the first 1,000 calibrated the sampler), for a total of 12,000 posterior samples. We based our inference about the importance of the hypothesized drivers of change in abundance on three lines of evidence: (1) the relative variable importance of each hypothesis (i.e., WAIC model weights), (2) the posterior probability of each hypothesis based on marginal likelihood estimates (Burkner, 2017), and (3) the sign, magnitude, and uncertainty in the parameter estimates representing each hypothesis in SD units. We performed two sensitivity analyses to determine whether our findings were robust to our assumptions: (1) we re-ran each model using uncorrected historical abundance estimates, and uncorrected average body-size and age for each population, and (2) we ran 1,000 iterations of each model - each iteration using a random point estimate of selectivity-corrected annual historical abundance - to account for uncertainty in our historical estimates. These revealed that model results are robust to our assumptions (SI, section I). All analyses were performed in R (R Core Team, 2018) using the "boot," "brms," "lme4," and "purrr" packages.

To examine whether populations have undergone larger changes in abundance than modern era data suggest, we quantified the magnitude of change in abundance for each population between the recent (2007–2014) period and both: (i) current baseline (1960–1967) and (ii) historical (1913–1923) periods (SI, section J).

3 | RESULTS

The total number of wild adult sockeye returning to the Skeena River in recent years is 75% lower than during historical times. The arithmetic mean annual abundance of wild fish in recent (2007–2014) years is 469,000 (range = 175,000–700,000), compared to 1,783,000 (range = 710,000–3,200,000) one century ago; production of sockeye from Babine Lake spawning channels has largely offset the long-term decline in wild fish (Figure 2).

Of 3,400 scales analyzed, 69% (2,354) were successfully assigned to a population, and 85% of these fish originated in the Skeena River. Within the Skeena, 13 populations were identified; all have declined in abundance over the last century (median = –82%), some by more than 90% (Table 1). For example, Motase and Sustut historically averaged ~40,000 and ~42,000 sockeye, respectively, while recently they average ~600 and ~1,600, respectively (Figure 3). Other populations, such as Bear (–56%) and Ecstall (–61%), have experienced smaller proportional declines. However, comparisons within the modern era (1960s to present), suggest that only 7 of 13 populations have declined (median = –6%). Population diversity also has shifted between time periods, such that the proportion of all wild fish returning to the Skeena River that are not from the Babine population has declined by 1/4 (from 33% one century ago, to 25% in recent years). Spawning channels on Babine Lake now produce roughly 70% of all sockeye returning to the Skeena River.

We found the strongest statistical support for the hypothesis that fisheries selectivity drives differences in the magnitude of decline among populations (Table 2). Declines were greatest for populations with larger body sizes; there was a 30% difference (96% compared to 66%) in rates of decline between populations with the largest and smallest body-size, respectively. For each SD unit increase in body-size (i.e., 1.8 cm), there was a predicted 7.4% greater decline in abundance, compared to 5.4% and 5.0% for each SD increase in age and migration distance, respectively. Rates of decline also tended to be greater in populations with older ages, and longer migrations, whereas rates of decline tended to be lower in populations with greater habitat degradation (Figure 4).

4 | DISCUSSION

Using modern molecular tools and century-old fish scales we show that wild sockeye salmon populations in Canada have declined more over the last century than are currently recognized. Specifically, our findings indicate that: (1) wild populations in the Skeena watershed have declined in abundance by between 56% and 99% since 1913; such diminishment is much greater than that revealed by recent (1960 to present) population data and (2) the populations that declined most had larger body-size, suggesting that fisheries selectivity may have contributed to variation in declines among populations. We acknowledge that salmon populations exhibit large variation in abundance over centuries, even in the absence of human impacts (Rogers et al., 2013). Regardless of the underlying mechanisms driving the change, the utility of our historical perspective is that it shifts modern era abundance data for Skeena sockeye back to a time before they incurred significant losses from commercial fisheries, and expands our

TABLE 1 Skeena River sockeye salmon populations identified in genetic analyses, total (catch + escapement) abundance estimates and genetic proportions of populations during the historical (1913–1923) and recent (2007–2014) periods, the percent change in historical abundance compared to the recent period, and population metrics used in hypothesis tests (note: Bear and Slamgeesh populations were omitted in modeling due to low sample size)

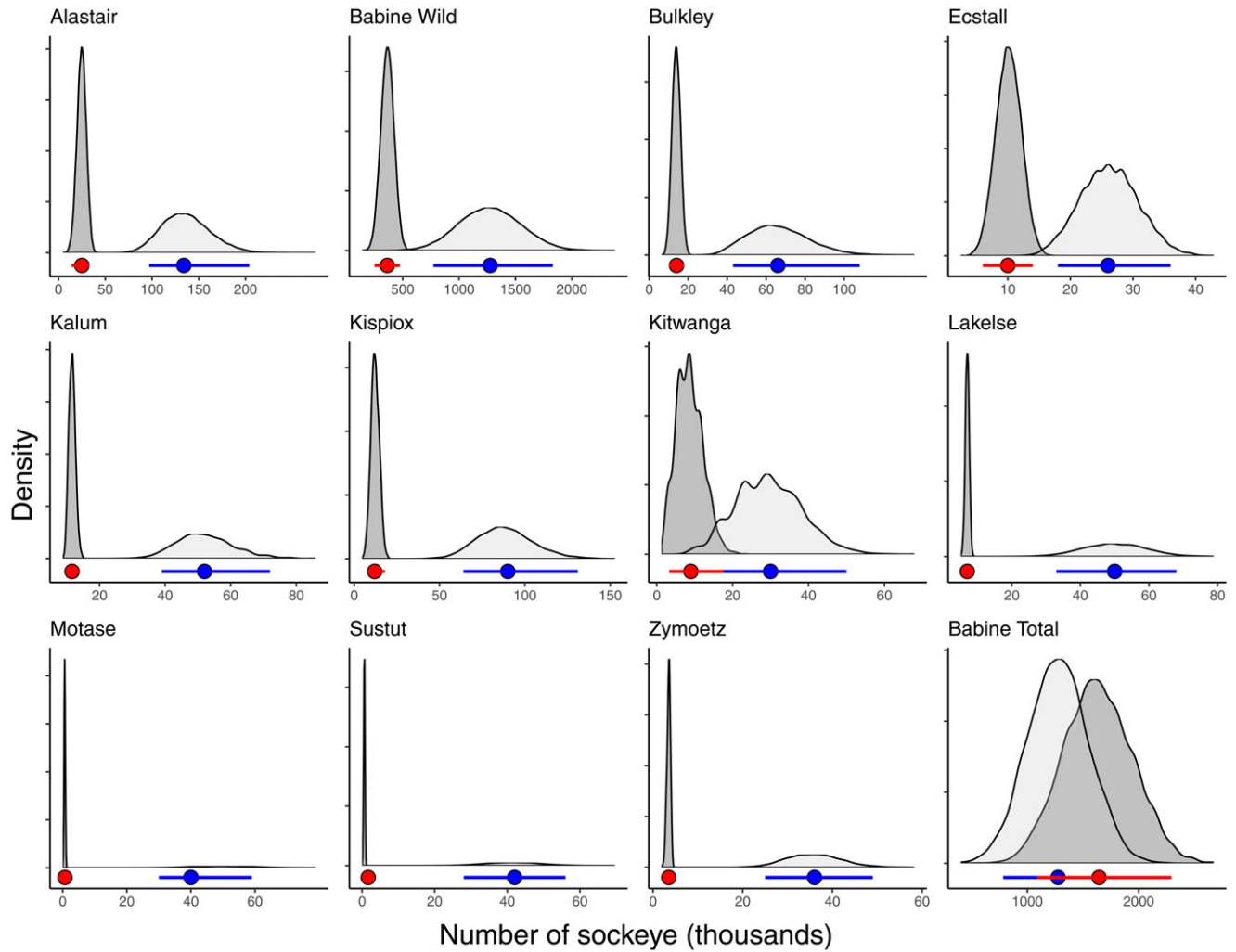| Population	Ref #	Historical abundance	Recent abundance	Abundance change (%)	Historical genetic proportion (%)	Recent genetic proportion (%)	Size*	Age*	Migration distance	Human footprint
Alastair	1	136,619	24,738	−82	9.2	2.0	61.57	5.11	98	4.35
Babine	2	1,275,739	364,790	−71	63.0	89.8	62.05	4.34	447	7.91
Bear	3	22,138	9,747	−56	0.6	0.6	–	–	–	–
Bulkley	4	66,232	13,978	−79	4.4	0.9	61.60	5.18	527	5.27
Ecstall	5	26,084	10,036	−61	1.2	0.3	60.17	4.50	68	5.55
Kalum	6	52,095	11,545	−78	3.2	1.3	64.92	4.73	161	5.47
Kispiox	7	88,935	12,123	−86	4.5	1.7	60.22	4.35	400	7.55
Kitwanga	8	29,515	8,672	−71	2.8	0.3	61.06	4.18	267	6.05
Lakelse	9	50,042	7,073	−86	4.2	1.0	62.76	4.56	131	19.26
Motase	10	39,649	590	−99	1.2	0.1	66.68	5.25	517	0.00
Slamgeesh	11	17,653	619	−97	0.6	1.1	–	–	–	–
Sustut	12	41,703	1,614	−96	2.1	0.5	66.68	4.82	584	0.00
Zymoetz	13	35,730	3,531	−90	3.2	0.5	63.07	4.48	253	2.47

FIGURE 3 Bootstrap distributions of abundance (in thousands of fish) for each Skeena River sockeye salmon population estimated during the historical (1913–1923; light gray) and recent (2007–2014; dark gray) period; Babine Total includes enhanced production from spawning channels plus Babine wild salmon abundance. Blue and red circles and horizontal lines are the arithmetic mean and 95% confidence intervals for historical and recent periods, respectively

TABLE 2 Results of Bayesian model fit describing each of our hypotheses: Size (average body length-at-maturity in cm), Footprint (human footprint as an average pressure score), Age (average age-at-maturity in years), Migration (migration distance in km), and the Null model (time-period), used to test for their influence on the change in abundance of wild sockeye salmon populations between historical (1913–1923) and recent (2007–2014) time periods. Our response variable (abundance) and Size- and Age-at-maturity coefficients were corrected for gill-net selectivity; all coefficients were standardized. Sample size for each model was 151 independent observations, and all models converged

Model	Estimate	Error	Lower 95%	Upper 95%	△WAIC	ωi	Probability
Size	−0.73	0.14	−1.00	−0.46	0.00	1.00	1.00
Footprint	0.51	0.14	0.24	0.79	12.80	0.00	.00
Age	−0.47	0.15	−0.75	−0.18	18.80	0.00	.00
Distance	−0.41	0.14	−0.69	−0.12	19.70	0.00	.00
Null	−1.98	0.15	−2.27	−1.70	21.90	0.00	.00

understanding of the production potential of populations that can inform status evaluations and rebuilding discussions.

Applying modern genetic techniques to ancient tissue is an emerging and powerful tool for understanding historical con-

texts for conservation, such as verifying population extinctions (Iwamoto, Myers, & Gustafson, 2012) or loss in diversity (Thompson et al., 2019). Our work utilized such genetic tools to build upon previous studies that used century-old
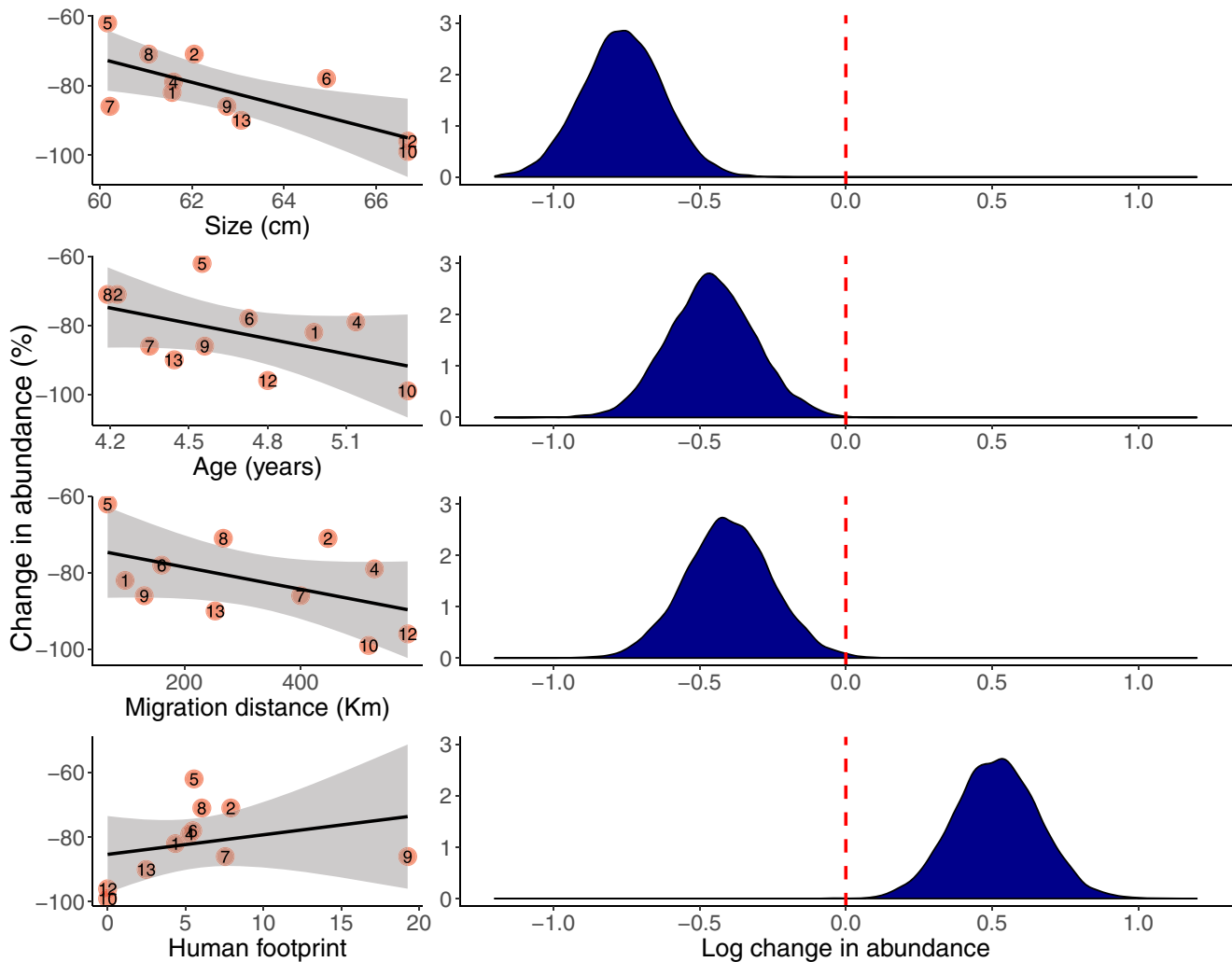
FIGURE 4 Left column: arithmetic mean change in abundance of Skeena River sockeye salmon from populations included in Bayesian models in relation to each of four hypothesis (Size, Age, Migration distance, and Human footprint) to explain the change in abundance between historical (1913–1923) and recent (2007–2014) time periods; numbers in red circles correspond to Figure 1; Bear (#3) and Slamgeesh (#11) were omitted due to low sample size. Right column: posterior distributions of Bayesian model results representing each hypothesis shown in the left column

salmon cannery data and reported similar declines for multiple species across the Northeast Pacific (Gresh, Lichatowich, & Schoonmaker, 2000). Salmon are fundamental components of ecosystems, and such loss of abundance may decouple interlinked systems dependent on salmon in several ways. First, diminished salmon returns have reduced nutrient subsidies that once were delivered to rivers throughout the watershed (Doughty et al., 2016), with potential impacts on wildlife that rely on salmon (Schindler et al., 2013). Second, the decline in abundance across all nonenhanced populations has undermined Indigenous peoples' food security throughout the rest of this vast watershed; many of these communities no longer catch sockeye due to low local abundance (Gottesfeld & Rabnett, 2008). Fewer salmon generally are associated with lower Indigenous fishery catches (Peterman, 1980), and diminished population diversity of salmon likely will compromise the stability of fisheries (Nesbitt & Moore, 2016).

Finally, the disproportionate loss in abundance from larger-bodied, older-aged, populations may have eroded the biocomplexity and stability of the Skeena sockeye aggregate by homogenizing size- and age-at-maturity. Loss in population diversity—and associated life-histories—can destabilize salmon stock complexes by reducing the range of potential responses to varying environmental conditions (Moore, Yeakel, Peard, Lough, & Beere, 2014; Schindler et al., 2010).

Fisheries selectivity of larger-bodied populations was the most probable driver of differences in rates of decline among populations over the last century, though age-at-maturity and migration distance also were associated with declines. Empirical comparisons among species show that large body-size and late-maturity are important predictors of fish vulnerability to fisheries (Hutchings, Myers, Garcia, Lucifora, & Kuparinen, 2012; Reynolds, Dulvy, Goodwin, & Hutchings, 2005). Within species, gill-net fisheries can induce

differential selection pressure such that large-bodied populations undergo higher mortality rates compared to small-bodied populations; a mechanism thought to have contributed to the disproportionate decline in sockeye from large-bodied beach-spawning populations in Alaska (Hamon, Foote, Hilborn, & Rogers, 2000). Indeed, differential catchability of gill-nets was the hypothesized driver of disproportionate declines in non-Babine populations in the Skeena prior to 1970 (Ricker & Smith, 1975). While selection pressure for large-bodied fish likely has weakened since 1950 due to the change towards less-selective gear (e.g., seine-nets; Kendall & Quinn, 2012), our results suggest that there may be a legacy effect of historical gill-net fisheries on Skeena sockeye populations. Body-size can be associated with vulnerability to other stressors, such as predators or temperature. Furthermore, as our results suggest, multiple factors (including age-at-maturity and migration distance) likely have contributed to large-scale declines in sockeye abundance and associated changes in population diversity. Surprisingly, habitat degradation failed to explain rates of decline. This may be because: (i) human footprint is a coarse measure of habitat loss (e.g., it excludes a "forest removal" score), and may be confounded by other factors that we did not consider or (ii) the Skeena watershed is relatively intact (Gottesfeld & Rabnett, 2008), and habitat has not been degraded sufficiently to impact salmon production.

Modern conservation policies for salmon (e.g., Canada's Policy for the Conservation of Wild Pacific Salmon; WSP) aim to maintain and rebuild distinct populations (DFO, 2005). The WSP requires the classification of extinction risk for populations based on metrics, like abundance trends, and such assessments are most reliable when the extent of decline is measured using long-term data (d'Eon-Eggertson, Dulvy, & Peterman, 2015). For sockeye populations in Canada, historical data begin after 1950 (COSEWIC, 2017). Our results identify larger declines in abundance than have previously been documented in this region (Price, English, Rosenberger, Mac-Duffee, & Reynolds, 2017). While it is difficult to set recovery targets when salmon productivity and abundances are naturally variable (Mantua et al., 1997; Rogers et al., 2013), our historical abundance estimates extend current time-series data to help inform assessments of population status, and contribute to rebuilding plan discussions.

Declines in wild Skeena sockeye abundance has been accompanied by an increase in production at the Babine Lake spawning channels. Fisheries that catch a mixture of wild and enhanced populations can complicate the conservation of diversity (Walters, Lichatowich, Peterman, & Reynolds, 2008; Wood, 2008). Given that annual commercial fishery decisions for Skeena sockeye are based on aggregate abundance targets, channel-enhanced production greatly increases the potential for overfishing of vulnerable wild populations (Walters et al., 2008). While the shared decline in all wild

populations that we report may indicate persistent overfishing during the period leading up to the 1950s (Pritchard, 1948; Ricker & Smith, 1975), this historical period may simply have been more favorable for salmon compared to the unproductive modern era. Indeed, oceanic-scale processes appear to have driven broad-scale changes in sockeye abundance across much of western North America over the last several decades (Peterman & Dorner, 2012).

Historical perspectives for exploited species are critical to understand the extent of decline in depressed populations; naturally, the better we understand the past, the more informed our decisions towards recovery will be (Bonebrake et al., 2010). Our analyses demonstrate that wild sockeye salmon in Canada are far more diminished than previously realized, and our results should help inform status evaluations and rebuilding plan discussions for depleted populations by expanding our understanding of their production potential. More generally, our study shows how genetic analyses of historical samples can provide insight into centennial-scale changes in population abundance and diversity.

REFERENCES

Argue, A. W., & Shepard, M. P. (2005). Historical commercial catch statistics for Pacific salmon (Oncorhynchus spp.) in British Columbia, 1828 to 1950. Canadian Technical Report of Fisheries and Aquatic Sciences 2601.

Beacham, T. D., Cox-Rogers, S., MacConnachie, C., McIntosh, B., & Wallace, C. G. (2014). Population structure and run timing of sockeye salmon in the Skeena River, British Columbia. *North American Journal of Fisheries Management*, *34*(2), 335–348. https://doi.org/10.1080/02755947.2014.880761

Bonebrake, T. C., Christensen, J., Boggs, C. L., & Ehrlich, P. R. (2010). Population decline assessment, historical baselines, and conservation. *Conservation Letters*, *3*(6), 371–378. https://doi.org/10.1111/j.1755-263X.2010.00139.x

Burkner, P. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*, 1–28.

COSEWIC. (2017). COSEWIC assessment and status report on the sockeye salmon Oncorhynchus nerka 24 designable units in the

Fraser River drainage basin in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottwa. Retrieved from http://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/srSockeyeSalmon2017e%2Epdf

Cox-Rogers, S., & Spilsted, B. (2012). Update assessment of sockeye salmon production from Babine Lake, British Columbia. Canadian Technical Report of Fisheries and Aquatic Sciences 2956. Ottawa, Canada.

d'Eon-Eggertson, F., Dulvy, N. K., & Peterman, R. M. (2015). Reliable identification of declining populations in an uncertain world. *Conservation Letters*, 8(2), 86–96. https://doi.org/10.1111/conl.12123

DFO. (2005). Canada's policy for conservation of wild Pacific salmon [online]. Fisheries and Oceans Canada, Vancouver, B.C. Retrieved from http://www.pac.dfo-mpo.gc.ca/fm-gp/species-especes/salmon-saumon/wsp-pss/docs/wsp-pss-eng.pdf

Doughty, C. E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E., … Svenning, J. S. (2016). Global nutrient transport in a world of giants. *Proceedings of the National Academy of Sciences*, 113(4), 868–873. https://doi.org/10.1073/pnas.1502549112

English, K. K., Peacock, D., Challenger, W., & Mochizuki, T. (2016). Review of north and central coast salmon escapement, catch, run size, and exploitation rate estimates for each salmon conservation unit for 1954–2014 [online]. Retrieved from http://skeenasalmonprogram.ca/libraryfiles/lib_1.pdf

Gaston, K. J., & Fuller, R. A. (2008). Commonness, population depletion and conservation biology. *TRENDS in Ecology and Evolution*, 23(1), 14–19. https://doi.org/10.1016/j.tree.2007.11.001

Gottesfeld, A. S., & Rabnett, K. (2008). *Skeena River fish and their habitat*. Portland, OR: Ecotrust.

Gresh, T., Lichatowich, J., & Schoonmaker, P. (2000). An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: Evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries*, 25(1), 15–21.

Gustafson, R. G., Waples, R. S., Myers, J. M., Weitkamp, L. A., Bryant, G. J., Johnson, O. W., & Hard, J. J. (2007). Pacific salmon extinctions: Quantifying lost and remaining diversity. *Conservation Biology*, 21(4), 1009–1020. https://doi.org/10.1111/j.1523-1739.2007.00693.x

Hamon, T. R., Foote, C. J., Hilborn, R., & Rogers, D. E. (2000). Selection on morphology of spawning wild sockeye salmon by a gill-net fishery. *Transactions of the American Fisheries Society*, 129(6), 1300–1315.

Hobbs, W. O., & Wolfe, A. P. (2007). Caveats on the use of paleolimnology to infer Pacific salmon returns. *Limnology and Oceanography*, 52(5), 2053–2061.

Holtby, L. B., & Ciruna, K. A. (2007). Conservation Units for Pacific salmon under the Wild Salmon Policy. Canadian Science Advisory Secretariat Research Document 2007/070.

Hughes, J. B., Daily, G. C., & Ehrlich, P. R. (1997). Population diversity: Its extent and extinction. *Science*, 278(5338), 689–692. https://doi.org/10.1126/science.278.5338.689

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

Iwamoto, E. M., Myers, J. M., & Gustafson, R. G. (2012). Resurrecting an extinct evolutionarily significant unit: Archived scales, historical DNA and implications for restoration. *Molecular Ecology*, 21, 1567–1582. https://doi.org/10.1111/j.1365-294X.2011.05419.x

Kendall, N. W., & Quinn, T. P. (2012). Quantifying and comparing size selectivity among Alaskan sockeye salmon fisheries. *Ecological Applications*, 22, 804–816.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, 78(6), 1069–1079.

Moore, J. W., Yeakel, J. D., Peard, D., Lough, J., & Beere, M. (2014). Life-history diversity and its importance to population stability and persistence of a migratory fish: Steelhead in two large North American rivers. *Journal of Animal Ecology*, 83(5), 1035–1046. https://doi.org/10.1111/1365-2656.12212

Nesbitt, H. K., & Moore, J. W. (2016). Species and population diversity in Pacific salmon underpin indigenous food security. *Journal of Applied Ecology*, 53(5), 1489–1499. https://doi.org/10.1111/1365-2664.12717

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution*, 10(10), 430–430.

Peterman, R. M. (1980). Dynamics of native Indian food fisheries on salmon in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(4), 561–566.

Peterman, R. M., & Dorner, B. (2012). A widespread decline in productivity of sockeye salmon (*Oncorhynchus nerka*) populations in western North America. *Canadian Journal of Fisheries and Aquatic Sciences*, 69(8), 1255–1260. https://doi.org/10.1139/F2012-063

Price, M. H. H., English, K. K., Rosenberger, A. G., MacDuffee, M., & Reynolds, J. D. (2017). Canada's Wild Salmon Policy: An assessment of conservation progress. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(10), 1507–1518. https://doi.org/10.1139/cjfas-2017-0127

Pritchard, A. L. (1948). Skeena River salmon investigations interim report. Appendix 3. Fisheries Research Board, Nanaimo, BC.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reynolds, J. D., Dulvy, N. K., Goodwin, N. B., & Hutchings, J. A. (2005). Biology of extinction risk in marine fishes. *Proceedings of the Royal Society of London B*, 272(1579), 2337–2344. https://doi.org/10.1098/rspb.2005.3281

Ricker, W. E., & Smith, H. D. (1975). A revised interpretation of the history of the Skeena River sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada*, 32, 1369–1381.

Rogers, L. A., Schindler, D. E., Lisi, P. J., Holtgrieve, G. W., Leavitt, P. R., Bunting, L., … Walsh, P. B. (2013). Centennial-scale fluctuations and regional complexity characterize Pacific salmon population dynamics over the past five centuries. *Proceedings of the National Academy of Sciences of the USA*, 110(5), 1750–1755. https://doi.org/10.1073/pnas.1212858110

Rosenberger, A. G., & Cox-Rogers, S. (2019). Abundance data for sockeye salmon (*Oncorhynchus nerka*) returning to Babine Lake during 2011–2018: unpublished. Smithers, BC.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, 465(7298), 609–613. https://doi.org/10.1038/nature09060

Schindler, D. E., Armstrong, J. B., Bentley, K. T., Jankowski, K. J., Lisi, P. J., & Payne, L. X. (2013). Riding the crimson tide: Mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters*, 9(3). Retrieved from http://doi.org/20130048

Shepard, M. P., & Withler, F. C. (1958). Spawning stock size and resultant production for Skeena sockeye. *Journal of the Fisheries Research Board of Canada*, *15*(5), 1007–1025.

Slaney, T. L., Hyatt, K. D., Northcote, T. G., & Fielden, R. J. (1996). Status of anadromous salmon and trout in British Columbia and Yukon. *Fisheries*, *21*(10), 20–35.

Soga, M., & Gaston, K. J. (2018). Shifting baseline syndrome: Causes, consequences, and implications. *Frontiers in Ecology and the Environment*, *16*(4), 222–230. https://doi.org/10.1002/fee.1794

Thompson, T. Q., Bellinger, M. R., O'Rourke, S. M., Prince, D. J., Stevenson, A. E., Rodrigues, A. T., … Miller, M. R. (2019). Anthropogenic habitat alteration leads to rapid loss of adaptive variation and restoration potential in wild salmon populations. *Proceedings of the National Academy of Sciences of the USA*, *116*(1), 177–186. https://doi.org/10.1073/pnas.1811559115

Walters, C. J., Lichatowich, J. A., Peterman, R. M., & Reynolds, J. D. (2008). Report of the Skeena Independent Science Review Panel. A report to the Canadian Department of Fisheries and Oceans and the British Columbia Ministry of the Environment. 144p.

Wood, C. C. (2008). Managing biodiversity of Pacific salmon: Lessons from the Skeena River sockeye salmon fishery in British Columbia. *American Fisheries Society Symposium*, *49*, 349–364.

SUPPORTING INFORMATION

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