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Portfolio simplification arising from a century of change in salmon population diversity and artificial production

Michael H. H. Price[1] | Jonathan W. Moore[1] | Brendan M. Connors[1,2] | Kyle L. Wilson[1] | John D. Reynolds[1]

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

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

Correspondence
Michael H. H. Price
Email: mhprice@sfu.ca

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Abstract

1. Population and life-history diversity can buffer species from environmental variability and contribute to long-term stability through differing responses to varying conditions akin to the stabilizing effect of asset diversity on financial portfolios. While it is well known that many salmon populations have declined in abundance over the last century, we understand less about how different dimensions of diversity may have shifted. Specifically, how has diminished wild abundance and increased artificial production (i.e. enhancement) changed portfolios of salmon populations, and how might such change influence fisheries and ecosystems?
2. We apply modern genetic tools to century-old sockeye salmon *Oncorhynchus nerka* scales from Canada's Skeena River watershed to (a) reconstruct historical abundance and age-trait data for 1913–1947 to compare with recent information, (b) quantify changes in population and life-history diversity and the role of enhancement in population dynamics, and (c) quantify the risk to fisheries and local ecosystems resulting from observed changes in diversity and enhancement.
3. The total number of wild sockeye returning to the Skeena River during the modern era is 69% lower than during the historical era; all wild populations have declined, several by more than 90%. However, enhancement of a single population has offset declines in wild populations such that aggregate abundances now are similar to historical levels.
4. Population diversity has declined by 70%, and life-history diversity has shifted: populations are migrating from freshwater at an earlier age, and spending more time in the ocean. There also has been a contraction in abundance throughout the watershed, which likely has decreased the spatial extent of salmon provisions to Indigenous fisheries and local ecosystems. Despite the erosion of portfolio strength that this salmon complex hosted a century ago, total returns now are no more variable than they were historically perhaps in part due to the stabilizing effect of artificial production.
5. *Policy implications*. Our study provides a rare example of the extent of erosion of within-species biodiversity over the last century of human influence. Rebuilding a diversity of abundant wild populations—that is, maintaining functioning portfolios—may help ensure that watershed complexes like the Skeena are robust to global change.

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KEYWORDS
artificial production, biodiversity loss, conservation genetics, fisheries, historical ecology, population diversity, portfolio effects, salmon abundance

1 | INTRODUCTION

The conservation of common species often is poorly aligned with extinction-focused assessments (Gregory et al., 2005). For example, roughly 95% of the loss in abundance among the world's birds derives from <10% of species, and the vast majority of these are assessed as least concern by the International Union for the Conservation of Nature (Baker et al., 2019). Likewise, the diversity in life-history characteristics and population processes within and among populations is far greater than among species (Hughes et al., 1997), yet global biodiversity assessments typically are species focused (e.g. Maxwell et al., 2016); such emphasis can substantially underestimate the changing state of nature (Luck et al., 2003). Abundance and diversity within populations are important conservation assets independent of global extinction risk (Balmford et al., 2003). Indeed, abundant species and their diverse populations disproportionately influence ecosystems (Gaston et al., 2018).

Biodiversity has many dimensions that contribute multiple benefits to humanity (Morris et al., 2014). One key benefit of biodiversity is that it helps stabilize ecosystem processes and functions, thereby bestowing resilience to environmental change. Such stability can arise through portfolio effects, where the aggregation of asynchronous dynamics dampens variability (Doak et al., 1998; Figge, 2004). Accordingly, portfolio effects can be stronger in systems with higher (a) richness—the number of species or populations in the system, (b) evenness—the proportional distribution of abundance or mass among the units (e.g. populations) of biodiversity and (c) asynchrony—the different responses of biodiversity to environmental forcing through time (Doak et al., 1998). For example, the intact habitat complexes of southwestern Alaska support high levels of population richness and asynchrony in sockeye salmon *Oncorhynchus nerka* that, in turn, stabilize commercial fishery catches (Schindler et al., 2010). There also is a growing appreciation of diversity among individuals, which can contribute to population-level resilience. For example, a diversity of life histories (e.g. different ages-at-maturity) within a population can spread risk across the demographic structure of that population, thereby buffering it from environmental variation over time (Greene et al., 2010; Moore et al., 2014). The spatial distribution of biodiversity can further influence the beneficial extent of that diversity, such as the degree to which consumers can access consistent prey resources across space and time (e.g. Deacy et al., 2016; Nesbitt & Moore, 2016). Thus, understanding the potential long-term shifts in the dimensions of biodiversity is a key frontier for conservation science.

Pacific salmon *Oncorhynchus* spp. are common and abundant species with substantial population and life-history diversity (Groot & Margolis, 1991). However, there is a growing appreciation that salmon have been undergoing major shifts in the dimensions of their diversity due to human activities. Most apparent is the decline in abundance and extinction of many populations in southern portions of their range resulting from habitat loss and over-exploitation (Gustafson et al., 2007; Slaney et al., 1996). In response to decreasing abundance, artificial production (i.e. enhancement) programmes—such as hatcheries and spawning channels—have increasingly been initiated. This enhancement may increase abundances for some populations but also can erode local diversity (Naish et al., 2008), homogenize life-history traits (Satterthwaite & Carlson, 2015) and further erode wild salmon abundances through competition in the ocean (Connors et al., 2020) or the subsidization of fisheries (Meffe, 1992). Life histories also are shifting with climate change (Oke et al., 2020). While several studies have documented shifts in dimensions of salmon diversity over the last several decades (e.g. Carlson & Satterthwaite, 2011; Moore et al., 2010), it has remained a challenge to understand potential changes over longer periods, such as the last century of major human impacts.

Here, we study Canada's Skeena River watershed to ask: how has sockeye salmon diversity changed over the last century of enhancement and other human activities (e.g. fishing and habitat alteration) and how might such change affect current fisheries and ecosystems? We use modern genetic tools with century-old fish scales to (a) reconstruct historical abundance and age-trait data for the 1913–1947 time period to compare with contemporary information, (b) quantify changes in population and life-history diversity and the role of enhancement in population dynamics, and (c) quantify the risk to fisheries resulting from observed changes in diversity and enhancement. Our results demonstrate substantial loss in abundance and diversity of wild sockeye populations over the last century. While enhancement has offset declines in wild populations and maintained aggregate abundances—which underpins the Skeena commercial fishery—loss in abundance from wild populations undermines food security and ecosystem provisions throughout much of the watershed.

2 | MATERIALS AND METHODS

The Skeena watershed is composed of 31 sockeye Conservation Units (CU; Holtby & Ciruna, 2007), which are grouped into 13 population complexes (Price et al., 2019; Figure 1; hereafter referred to as *populations*). Commercial fishing for sockeye began at the mouth of the Skeena River in 1877 (Wood, 2008), and a scale-collection programme began in 1912. We sampled scales from 35 to 50 fish from the collection for each of nine fishing weeks from years 1913, 1916, 1918–1923, 1933, 1935, 1937, 1943, 1945 and 1947 for a total of 5,400 scales. Sampling either began 1 week late or ended 1–2 weeks early in some years (i.e. 1913, 1916, 1918, 1920, 1937, 1943 and 1945) such that scales were unavailable

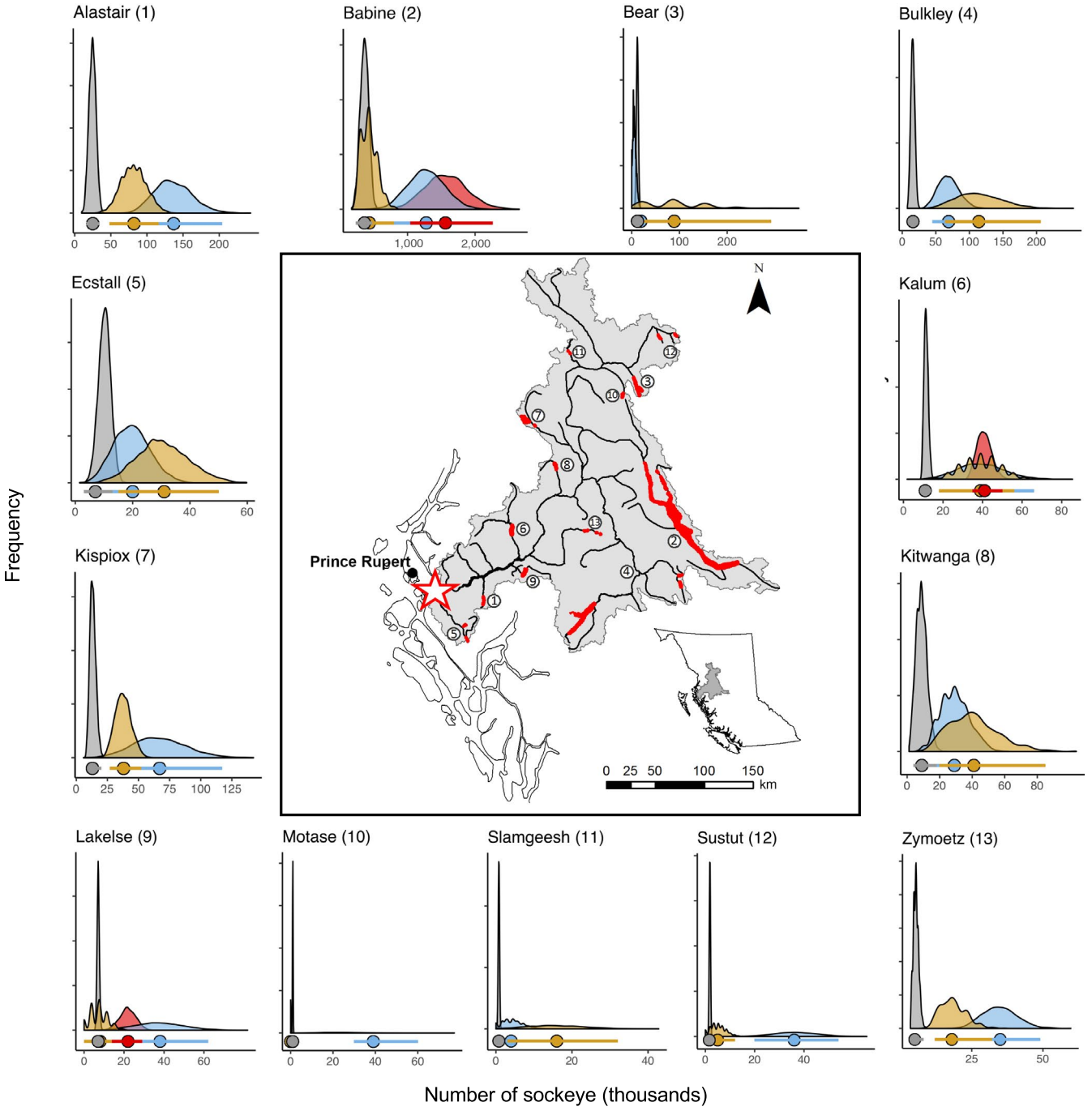

FIGURE 1 Skeena River watershed and sockeye salmon population abundances. Inset: Skeena River watershed showing locations of each sockeye salmon population complex (numbers 1–13) identified in genetic analyses, with associated nursery lakes (in red), and approximate location of historical scale sample collection and current Skeena Tyee Test Fishery (white-filled red star). Border: estimated population abundance (in thousands) during the 1913–1923 (blue), 1933–1947 (orange) and 2010–2017 (grey) time periods. Red distributions (#2, 6, 9) denote total (wild plus enhanced) abundance during 2010–2017. Circles and horizontal lines are the arithmetic mean and 95% bootstrapped confidence intervals

in some weeks. Because these omissions likely were due to low availability of fish to fisheries, we consider the implications to our analyses negligible. We digitally photographed one scale per fish, and aged each scale by annuli counts (Gilbert, 1913). DNA was extracted from scales, genotyped at up to 12 microsatellite loci, and individuals were assigned to population via genetic stock identification (see Appendix S1). All scale samples were from existing collections and therefore exempt from Simon Fraser University's Animal Care Protocol.

We estimated annual historical (1913–1947) numbers (i.e. catch plus spawning fish, which throughout we refer to as *abundance*) of sockeye at the population level in a four-step process (Figure S1; Price et al., 2019), which included three year- and week-specific data inputs: (a) Annual abundance derived from catches (Argue & Shepard, 2005)

and exploitation rates (Shepard & Withler, 1958) reconstructed from Skeena cannery and fishery data. (b) Daily counts of sockeye entering the Skeena River from each of 7 years (2011–2017), partitioned into nine fishing weeks equivalent to the historical scale-sampling periods. (c) Weekly proportions of Skeena-origin populations identified in scales. Briefly, with these data, we randomly drew from one of the 7 years of weekly abundance proportions, multiplied these by a given historical year's aggregate abundance, then multiplied these weekly abundances by population proportions, and summed population abundances across weeks. We repeated these steps 50,000 times, and then derived a median abundance estimate for each population for each historical year.

Estimates of total abundance during the modern (2004–2017) era are available from PSF (2020) and English et al. (2018), and detailed in our Supporting Information. Major enhancement projects have occurred since 1970 for three sockeye populations: Babine, Kalum and Lakelse; minor enhancement efforts had occurred for at least two populations (Lakelse and Babine) prior to 1970, with little success (Foerster, 1968). To estimate wild-only abundance for the Babine population, we combined annual abundance estimates for the four wild Babine CUs. Annual estimates of wild fish for Kalum were derived from run-reconstructions detailed in the citations above, but with spawning channel contributions removed (Appendix S2). Finally, to estimate wild-only abundance for the Lakelse population, we substituted years 2002–2009 (pre-enhancement) for 2010–2017 (post-enhancement) because we could not disaggregate enhanced contributions for the latter years, which greatly increased the abundance of sockeye returning to Lakelse.

We quantified the spatial contraction of population abundance throughout the Skeena watershed, and the potential loss of fish available to in-river fisheries and wildlife. This required estimates of in-river abundance for each population for the two time periods: (a) historical (1913–1947; quantified by subtracting commercial catch from our reconstructed historical abundance estimates) and (b) modern [2004–2017; quantified by adding annual in-river fishery catch (English et al., 2017) to spawning escapement (wild and enhanced fish combined)]. We then compared the change in in-river abundance between time periods for each population (tributary system), and each main-stem section of the Skeena River between populations, by subtracting each population's abundance downstream of each main-stem river section from the total in-river abundance.

We used several sources of age-at-maturity data depending on our question. For example, we used age data from fish (aggregate of populations) caught in commercial fisheries, as reported in annual fisheries reports for the years 1916–1956 (Province of British Columbia, 1957), and from fish caught in the Tyee Test Fishery for the years 1973–2016, to estimate changes in life-history diversity and age-at-maturity. We used data from fish (identified to population) collected from commercial fisheries for 1913–1947, and from the Tyee Test Fishery for 2000–2013 to estimate changes in age traits within populations, and to explore the strength of salmon portfolios during various time periods. Because sockeye returning to the Skeena River during 1877–1950 were caught exclusively by linen gill-nets in commercial fisheries, we applied a correction factor to historical age data based on the selectivity of sockeye captured during the modern era by gill-nets in the Tyee Test Fishery to more accurately characterize the historical proportion of ages-at-maturity (Appendix S3). When describing various age-related life-history expressions (i.e. age traits), we use the European designation where the first number denotes the years spent in freshwater, and the second number denotes the years in the ocean (e.g. 1.2 represents 1 year in freshwater and 2 years in the ocean, and 1.*x* represents fish spending 1 year in freshwater and any number of years in the ocean).

We quantified the extent to which diversity among populations in abundance and life history has changed over time (historical versus modern era). Specifically, we calculated Pielou's Evenness, *E*, as a measure of diversity each year:

$$E = H/\ln S \tag{1}$$

where *S* is the number of populations ($n = 13$) or age traits ($n = 4$), and *H* is the Shannon diversity index:

$$H = -\sum_{i-1}^{S} p_i \ln p_i \tag{2}$$

where *p* is the proportional contribution of group *i* such that $\sum_{i}^{S} p_i = 1$ (Oksanen et al., 2019). Evenness is bounded between 0 and 1, with 1 being a completely even distribution among populations (*S*). To examine how enhancement of populations post-1970 has affected both population- and age-diversity, we calculated evenness separately using 'wild-only' and 'total' (enhanced plus wild) abundances; these abundances were applied separately to age-trait proportions to generate annual estimates of each age trait before calculating evenness.

We explored whether the strength of salmon portfolios in the Skeena has changed over time by calculating portfolio effect for each period (1913–1923, 1933–1947, and 2010–2017); here we compared the coefficient of variation (CV; defined as the ratio of the standard deviation to the mean) for the Skeena sockeye complex as a whole (i.e. meta-population CV) to the arithmetic mean CV for individual component population abundances and age traits (i.e. average CV). We chose the 8-year period of 2010–2017 for recent years to be comparable with the eight data-years of 1913–1923; Ecstall and Motase populations were excluded due to lack of recent data.

With these data, we then quantified the individual and combined consequences of (a) portfolio effects, (b) population abundances, and (c) enhancement, on the probability of commercial fishery closures for sockeye returning to the Skeena over the three time periods. Annual commercial fishery openings for Skeena sockeye currently are based on an aggregate abundance target of 1.05 million fish (900,000 spawning escapement plus 150,000 for Indigenous fisheries; DFO, 2003), below which the mixed-stock commercial fishery is closed. We simulated annual pre-fisheries abundances of wild sockeye in each time period by drawing from a log-normal distribution with a bias-corrected mean and standard deviation (i.e. CV, equal either to the meta-population CV or average CV). We repeated this for each time period across 10,000

Monte Carlo trials, and then calculated the proportion of trials where system-wide abundance fell below the aggregate abundance threshold of 1.05 million fish. For the recent period, we simulated wild-only and total (wild plus enhanced fish combined) abundances separately to quantify the degree to which enhancement may influence the probability of commercial fishery closures. Admittedly, our simulation ignores the potential confounding effects of forecast error and changes in exploitation on subsequent population dynamics.

All analyses were performed in R (R Core Team, 2020) using the BOOT, ECOFOLIO, and VEGAN packages.

3 | RESULTS

The total number of wild adult sockeye returning to the Skeena River during the modern era is 69% lower than during the historical era of commercial fishing. All wild populations have declined (median = −80%) over the last century, several by more than 90%, and headwater populations (i.e. situated upstream of Babine; #2) have declined the most (average: −93%; Figure 1). While most populations had declined in abundance by 1933–1947, five populations had increased, but then declined over the modern era. For example, the Bear population (#3) increased from an average of 22,000 to 89,000 (range: 0–415,000), and Bulkley (#4) from 69,000 to 114,000 (range: 25,000–276,000). Population composition also has shifted between periods such that the Babine population once accounted for 68% of all wild sockeye returning to the Skeena, declined to 48% by 1933–1947, then increased to 75% recently. When enhanced fish are combined with wild fish, Babine now accounts for 91% of all sockeye returning to the Skeena watershed (Figure 2a).

Skeena sockeye currently exhibit the 10 age traits identified in scales collected one century ago, of which 99% are one of four dominant freshwater/ocean ages: 1.2, 1.3, 2.2, or 2.3 (Figure 2b; Appendix S4). Two additional contemporary life histories—fish that reared in freshwater lakes for 3 years and returned to spawn after either 2 (3.2) or 3 (3.3) years in the ocean—were not among those caught in historical fisheries. While the average age (freshwater plus ocean) of populations has not changed, there has been a shift in age composition. For example, the proportion of wild fish with the *x*.3 (longer residency in the ocean) life history has increased from 37% to 47% (Figure 2b). When enhanced fish are included, 51% of sockeye spent 3 years in the ocean, and the proportion of fish in a given year migrating to the ocean after one freshwater year increased from 87% to 96% (Figure 2c).

Individual contributions of wild populations to aggregate abundances have greatly diminished. For example, mean evenness of wild population contributions to overall abundances declined by 35% (from 0.62 to 0.40) between the historical and modern era. When enhanced fish are combined with wild fish, the decline over the last century is even greater (evenness = 0.18 in the recent period, a 70% total decline; Figure 3a). The evenness of age traits declined by 19% (from 0.68 to 0.55) during the period since 1973, and inclusion of enhanced fish only modestly reduced the evenness further (to 0.54; Figure 3b).

The extent to which the population portfolio dampened interannual variation in abundance has eroded over the last century. For example, portfolio strength during 1913–1923 resulted in aggregate returns that were 2.04 times more stable than if the system had been composed of a single population with homogeneous dynamics (CV reduced from 1.01 to 0.50). For 1933–1947, the comparable value was 1.48 (CV reduced from 0.96 to 0.65). The benefits of population diversity for stabilizing returns have largely disappeared in recent (2010–2017) years (i.e. aggregate returns now are only 1.10 times more stable—CV reduced from 0.57 to 0.52; Figure 4a). Had

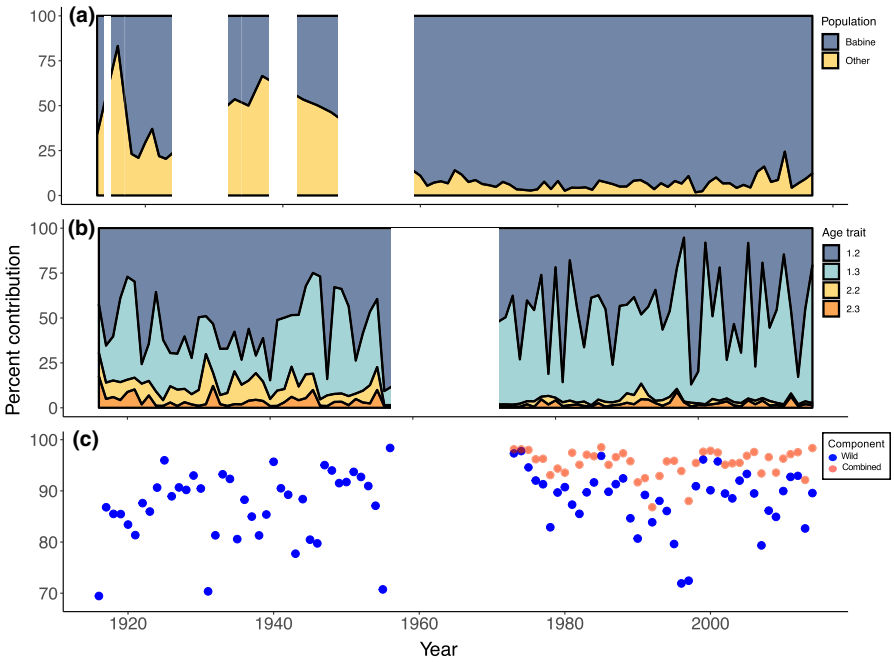

FIGURE 2 Long-term change in sockeye salmon population and life-history diversity. (a) Percentage of population abundances, where *Other* combines all populations except Babine. (b) Percentage of the four dominant age traits. (c) Percentage of juveniles that emigrated to the ocean after 1 year in freshwater; blue and red circles denote wild fish, and wild and enhanced fish combined, respectively (i.e. for the years since enhancement began, data for each year are shown twice: once for wild fish, and once for wild and enhanced fish combined). Information gaps (white bars) differ in plots a and b because the data are derived from different sources (a: historical scale collection; b: annual government fishery reports)

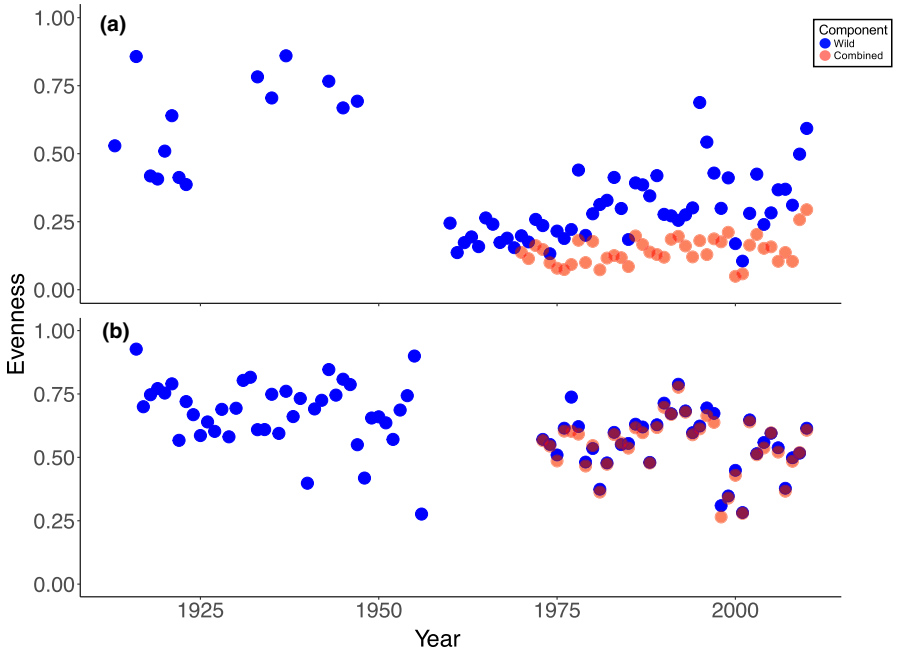

FIGURE 3 Long-term change in sockeye salmon diversity. (a) Evenness in abundance across individual populations. (b) Evenness in age traits across aggregated populations. Blue and red circles denote wild fish, and wild and enhanced fish combined, respectively (i.e. for the years since enhancement began, data for each year are shown twice: once for wild fish, and once for wild and enhanced fish combined)

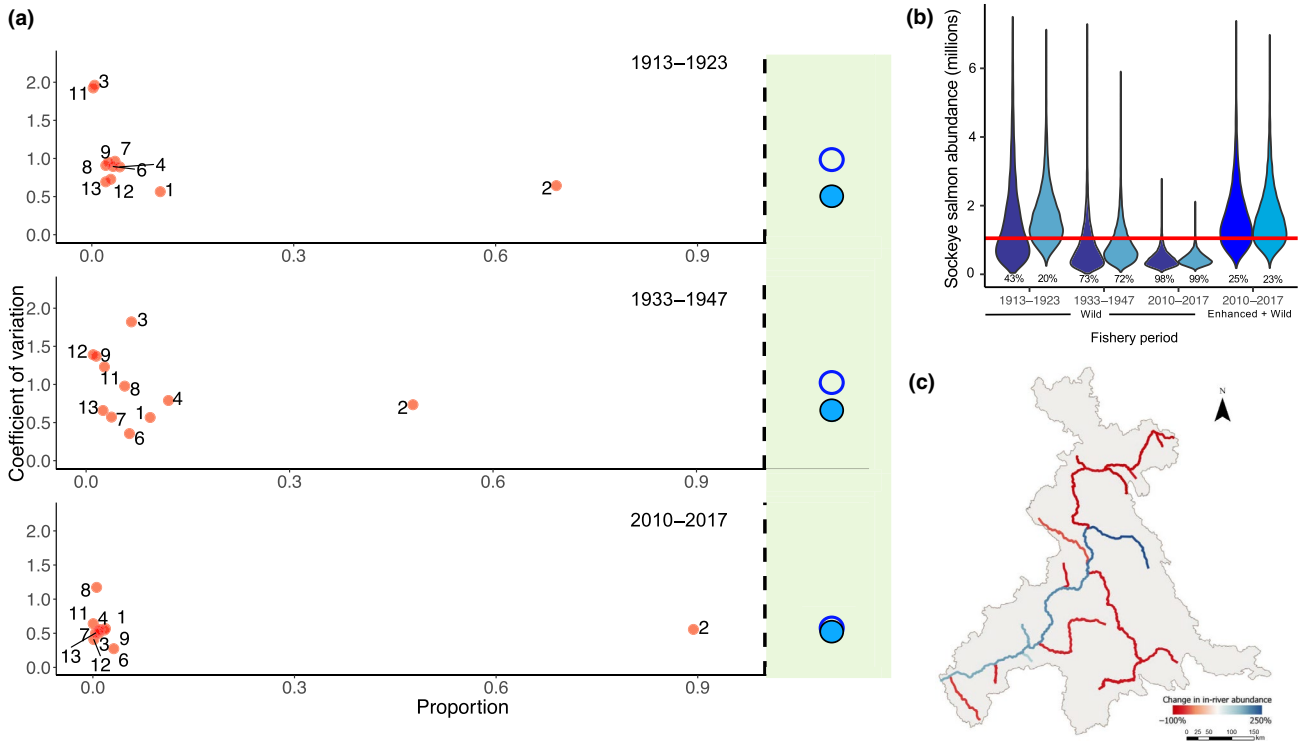

FIGURE 4 Changes in sockeye salmon population diversity and their influence on fisheries and ecosystems. (a) Portfolio effect: each red-filled circle represents the coefficient of variation (CV) of abundance (wild and enhanced combined) across years for each time period as a function of the proportional contribution of each population to total returns; numbers correspond to Figure 1. Shown within green bar is the estimated CV based on the average of the CVs of the different populations (dark-blue circle), and the measured meta-population CV of the entire Skeena sockeye complex (filled light-blue circle). The difference between the estimated and measured CV is a measure of the magnitude of reduction in variation due to the portfolio effect. (b) Simulated abundance and risk of commercial fishery closures for each time period assuming either the average CV (dark blue) or meta-population CV (light blue). Red solid line is the aggregate abundance target of 1.05 million, above which the commercial fishery begins. Values below each distribution are the percentage of simulation trials that were below the abundance target. (c) Change in in-river sockeye abundance (number of fish in the Skeena River and tributaries after marine and lower river commercial fishery removals) between the historical (1913–1947) and modern (2004–2017) eras

the Skeena sockeye complex lacked the dampening effects that population diversity provides (i.e. using average versus meta-population CV), commercial fishery closures would have occurred 42% of the time (a 55% increase compared to a diverse system) during the 1913–1923 period, and 74% of the time (3% increase) during 1933–1947 (Figure 4b). While commercial fisheries based on wild fish now would be closed in at least 98% of years because of low abundance, enhanced sockeye production has effectively replaced the loss in wild fish and sustained commercial fisheries.

Finally, the observed changes in abundance are associated with spatial contraction of sockeye abundance throughout the Skeena watershed. Specifically, wild populations have undergone major declines in tributaries (41%–90% loss) and headwater main-stem sections (75%–87% loss; Figure 4c). Enhancement sustains abundance primarily in one major tributary (Babine) and the main-stem river downstream of Babine.

4 | DISCUSSION

Conserving a diversity of populations and their varied life histories can help buffer ecosystems from environmental change (Schindler et al., 2015). We applied modern genetic tools to century-old fish scales to reveal substantial loss in abundance and biodiversity of wild sockeye populations over the last 100 years for Canada's second largest salmon watershed, the Skeena River. While artificial enhancement has returned aggregate abundances to historical levels, declines in abundance across wild populations have increased the dependency of fisheries on enhanced fish, potentially widening the trade-off between exploitation and conservation of diversity in the watershed (Walters et al., 2008; Wood, 2008). Consequently, the Skeena has lost much of the stabilizing portfolio effects that population diversity had provided a century ago. Furthermore, there has been a spatial contraction in abundance throughout the watershed, which likely decreases the provisioning of salmon to local ecosystems and Indigenous fisheries.

Artificial salmon production has returned abundances to what they were a century ago, but such enhancement may compromise diversity across the watershed. While the abundance of all wild sockeye populations in the Skeena now is substantially lower than during the historical era, some populations—such as Babine—had already declined by the 1940s, which prompted the development of spawning channels by 1970 to rebuild diminished abundance (McDonald & Hume, 1984). Enhancement has since increased annual total sockeye returns to 99% of the estimated abundance of one century ago, which has renewed opportunities for commercial marine fisheries and Indigenous fisheries in Babine Lake and the main-stem river downstream. Despite these benefits to fisheries, enhanced production may impact wild Skeena populations in at least four ways: (a) Pathogen transfer from enhanced to wild fish could decrease survival. While there historically have been disease outbreaks at Babine spawning channels (Traxler et al., 1998), improvements may have decreased these risks. (b) Straying of enhanced fish may erode local adaptations in wild populations due to introgression (Naish et al., 2008). Sockeye salmon are known to spawn near their river-of-origin, and different Skeena populations remain genetically distinct (Beacham et al., 2014), yet enhanced fish may stray into wild spawning streams within the Babine system given the close proximity of spawning channels to neighbouring wild streams. (c) Enhanced fish could compete with wild fish (Peterman, 1982). However, there is no evidence that the production of enhanced sockeye has reduced the survival of wild populations (Price & Connors, 2014). (4) Enhanced fish could elevate mortality of wild fish as a result of their incidental capture in mixed-stock fisheries targeting enhanced fish (Meffe, 1992). Increases in aggregate abundance since 1970 are thought to have exacerbated the trade-off between mixed-stock fisheries catch and the protection of wild population diversity in the watershed (Walters et al., 2008; Wood, 2008). All wild populations likely were over-exploited in the decades immediately following spawning channel development due to their co-migration with enhanced sockeye (Walters et al., 2008). However, Canadian aggregate mixed-stock exploitation has declined in recent years [from 46% (1970–2009) to 28% (2010–2017); English et al., 2018], and may be sustainable for some wild populations. Thus, the degree to which enhancement now compromises sockeye diversity in the Skeena remains unclear.

Life-history diversity has remained relatively stable since the historical era, though there have been notable shifts in age composition. Sockeye in the Skeena currently display all age traits identified in scales that were collected one century ago, which may indicate the persistence of diverse habitats in the watershed (Waples et al., 2001). Nonetheless, fish are remaining longer in the ocean, with an increase (from 36% to 51%) in the proportion of fish that rear in the ocean for 3 years. Similar increases have been reported for sockeye from the Fraser River and Bristol Bay over the recent period (Cline et al., 2019; Ruggerone & Connors, 2015); increased biomass of salmon in the North Pacific Ocean and shorter residency in freshwater are thought to contribute to these trends. Our data also show that Skeena sockeye now spend less time in freshwater (e.g. decrease from 13% to 4% in the proportion of fish that rear for 2 years). While the reduced duration of freshwater residency across wild populations may be influenced by increasing lake temperatures (as has occurred in Alaska; Cline et al., 2019), enhancement of Babine fish is further increasing the overall prevalence of this life history (Appendix S5). This change in age-structure—where most juveniles now emigrate to the ocean in the same year—increases the risk that an entire cohort will encounter unfavourable conditions (e.g. Moore et al., 2014), and may reduce the resilience of the Skeena sockeye complex to future environmental change.

Portfolio effects have largely eroded in the Skeena over the last century. Had the dynamics of the Skeena sockeye complex a century ago been characterized by the most simplified population portfolio (i.e. a single population), they would have been 2.04 times more temporally variable than was observed. This strength in portfolio is similar to the Bristol Bay sockeye complex, which hosts hundreds of populations from largely undisturbed habitat, and does not

have salmon enhancement (Schindler et al., 2010). By 1933–1947, portfolio strength in the Skeena had been reduced by one-third, yet the population complex still was 1.48 times more stable than if it had been composed of a single population. In recent years, the benefits of population diversity have nearly disappeared (i.e. aggregate returns now are only 10% more stable). Degraded portfolio performance is correlated negatively with anthropogenic impact on watersheds across western North America (Griffiths et al., 2014). However, even in a recently collapsed Chinook salmon *Oncorhynchus tshawytscha* system with extensive habitat degradation—where enhancement is thought to have significantly weakened the portfolio (Satterthwaite & Carlson, 2015)—the strength of the population portfolio since the mid-1980s is far greater than it is now for Skeena sockeye (Carlson & Satterthwaite, 2011), although there may be an inherent challenge in comparing across species. While enhancement has simplified the Skeena portfolio by tripling the abundance of sockeye returning to a single population since 2010—removal of enhanced fish from the analyses increased portfolio strength by a factor of five—declines in portfolio strength since the 1913–1923 period also were influenced by increased population synchrony (Appendix S5). Regardless of the mechanism, a notable consequence of the portfolio simplification is that commercial fisheries now depend on a single population that is largely composed of enhanced fish, whereas a diversity of populations sustained fisheries historically.

A simplified population portfolio should lead to an increase in variability of aggregate abundances. However, sockeye returns to the Skeena now are as stable as they were during the historical era despite a weakened portfolio. Such reduced variability may be because the aggregate's variability now is primarily influenced by a single population whose annual production is at least in part stabilized by artificial enhancement. While variability in population abundances also has decreased over the recent period, an inherent challenge in measuring change over long time periods such as ours is the different data collection methods used between eras. We used an admittedly coarse method to quantify population abundance during the historical era compared to higher precision methods of the modern era, which may inflate declines in portfolio strength between periods. However, when we compared the variability of populations between periods using genetic (rather than abundance) data, population variability remained lowest in the modern era (i.e. populations now are more stable than during either of the historical periods; Appendix S5). Indeed, sockeye populations in the Skeena have become more synchronized with one another, all but one (Babine) are at low levels of abundance, and perhaps are responding similarly to a low productivity phase that could be the result of reduced response diversity of these populations. Thus, despite the relative stability of sockeye returns to the Skeena over the recent period, the weakened portfolio may compromise its resilience to larger perturbations in the future.

The erosion of diversity in the Skeena is further expressed in the spatial contraction of salmon abundance throughout the watershed. Wild sockeye abundance has declined in all tributaries and headwater regions since the historical era, which—according to oral accounts—has compromised food security for Indigenous Peoples that rely upon these areas for subsistence fisheries (Cleveland et al., 2006; Gottesfeld & Rabnett, 2008). Furthermore, these tributaries are important corridors that provision salmon resources to local ecosystems. Such loss in abundance likely constrains foraging opportunities for wildlife dependent on salmon (Deacy et al., 2016), and lessens the overall delivery of salmon-derived nutrients to ecosystems (Gende et al., 2002), which can affect a large number of species (Walsh et al., 2020).

Our reconstruction of century-old portfolio performance provides a baseline for the recovery of a diminished watershed complex. Modern conservation policies for salmon, such as Canada's Policy for the Conservation of Wild Pacific Salmon, strive to maintain a diversity of populations (DFO, 2005). If the goal of fisheries management is to catch abundant channel-enhanced fish while conserving wild populations, increasing selectivity by moving a larger proportion of the fishery in-river and to terminal locations likely will improve conservation, though it may result in reduced catches (Freshwater et al., 2020). Prioritizing the rebuilding of wild salmon populations could mitigate such trade-offs, help increase fishing opportunities for Indigenous peoples that rely on wild populations and strengthen the sockeye portfolio within this now simplified watershed.

Our study provides a rare example of the extent of erosion of within-species biodiversity over a century of human influence. While the enhancement of salmon supports commercial fisheries, loss in abundance and diversity from wild populations has reduced the provisioning of salmon to local ecosystems and Indigenous fisheries throughout the watershed. What may be underappreciated is the lost stabilizing portfolio effects that this watershed complex hosted a century ago, which ultimately may weaken its resilience to increasingly variable environments. Conserving a diversity of abundant wild populations and their varied life histories—that is, maintaining functioning portfolios—may help ensure that watershed complexes like the Skeena are robust to global change.

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AUTHORS' CONTRIBUTIONS

M.H.H.P., J.W.M., B.M.C., K.L.W. and J.D.R. conceived the ideas and designed the methodology; M.H.H.P. collected the data; M.H.H.P.

and K.L.W. analysed the data; M.H.H.P. led the project and writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.n5tb2rbts (Price, 2021).

ORCID

Michael H. H. Price https://orcid.org/0000-0002-2909-8836
Kyle L. Wilson https://orcid.org/0000-0002-0870-0509
John D. Reynolds https://orcid.org/0000-0002-0459-0074

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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