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A synthesis of the coast-wide decline in survival of West Coast Chinook Salmon (*Oncorhynchus tshawytscha*, Salmonidae)

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This study was initially internally funded by Kintama Research Services as part of a separate research effort to assess the credibility of the critical period concept in Pacific salmon. In the course of assembling Strait of Georgia SAR data, we discovered that Chinook survival in many rivers of the Strait of Georgia region had fallen to levels well below those reported for Snake River Chinook. We developed a proposal and obtained funding from the US Dept. of Energy, Bonneville Power Administration, to cover staff time for coast-wide data collation, analysis and writing of this paper (Contract # 75025). The funder (BPA) played no role in the design of the study nor the conclusions reached and was not made privy to the specific contents of this manuscript prior to journal submission.

Abstract

We collated smolt-to-adult return rate (SAR) data for Chinook salmon from all available regions of the Pacific coast of North America to examine the large-scale patterns of salmon survival. For consistency, our analyses primarily used coded wire tag-based (CWT) SAR estimates. Survival collapsed over the past half century by roughly a factor of three to ca. 1% for many regions. Within the Columbia River, the SARs of Snake River populations, often singled out as exemplars of poor survival, are unexceptional and in fact higher than estimates reported from many other regions of the west coast lacking dams. Given the seemingly congruent decline in SARs to similar levels, the notion that contemporary survival is driven primarily by broader oceanic factors rather than local factors should be considered. Ambitious Columbia River rebuilding targets may be unachievable because other regions with nearly pristine freshwater conditions, such as SE Alaska and northern BC, also largely fail to reach these levels. Passive integrated transponder (PIT) tag-based SAR estimates available for Columbia River Basin populations are generally consistent with CWT findings; however, PIT tag-based SARs are not adjusted for harvest which compromises their intended use because harvest rates are large and variable. More attention is needed on how SARs should be quantified and how rebuilding targets are defined. We call for a systematic review by funding agencies to assess consistency and comparability of the SAR data generated and to further assess the implications of survival falling to similar levels in most regions of the west coast.

KEYWORDS

Columbia River, dams, delayed mortality, marine survival, smolt-to-adult return, Snake River

1 | INTRODUCTION

The abundance of salmon (family Salmonidae) in the North Pacific has reached record levels (Irvine et al., 2009; Ruggerone & Irvine, 2018; Schoen et al., 2017); however, most of the increase is in the two lowest valued species (pink, *Oncorhynchus gorbuscha*, and chum, *O. keta*) in far northern regions, at least in part due to ocean ranching (Ruggerone & Irvine, 2018). In contrast, essentially all west coast North American Chinook (*O. tshawytscha*) populations including Alaska are now performing poorly with dramatically reduced productivity (Dorner et al., 2017; Ohlberger et al., 2016).

The situation in North America is similar for most southern populations of coho (*O. kisutch*) (Logerwell et al., 2003; Zimmerman

Abbreviations: BC, British Columbia, Canada; CSS, Comparative Survival Study; CWT, Coded Wire Tag; PIT, Passive Integrated Transponder; PSC, Pacific Salmon Commission; SAR, Smolt-to-Adult Return Rate (Survival).

et al., 2015), sockeye (*O. nerka*) (Cohen, 2012; COSEWIC, 2017; Peterman & Dorner, 2012; Rand et al., 2012), and steelhead (*O. mykiss*) (Kendall et al., 2017). These poorly performing species are of higher economic value and the focus of indigenous, sport and commercial fisheries.

The historical pattern of declines in salmon abundance (steeper in the south, less so in the north) were originally assumed to reflect a freshwater anthropogenic cause because of the greater degree of freshwater habitat modification in the more populous southern regions (Allendorf et al., 1997; Nehlsen et al., 1991). The growing appreciation of ocean climate change (Hare et al., 1999; Mantua & Hare, 2002; Mantua et al., 1997) has brought an awareness of the role of the ocean in influencing salmon survival. As Ryding and Skalski (1999, p. 2374) noted two decades ago, "*It is becoming increasingly clear that understanding the relationship between the marine environment and salmon survival is central to better management of our salmonid resources*."

Unfortunately, our understanding of survival during the marine phase remains extremely limited, so there has been little change in management strategy beyond the essential first step of reducing harvest rates in the face of falling marine survival. The recent recognition of the decline in Chinook returns across essentially all of Alaska (ADF&G Chinook Salmon Research Team, 2013; Cunningham et al., 2018; Ohlberger et al., 2016; Schindler et al., 2013) and the Canadian portion of the Yukon River (Bradford et al., 2009), where anthropogenic freshwater habitat impacts are negligible, is another example of how simple explanations are potentially flawed. If survival across this vast swathe of relatively pristine territory is severe enough to seriously impact salmon productivity, then there is little hope that modifying freshwater habitat in more southern regions will support a newly productive environment for salmon.

Formal smolt-to-adult return (SAR) or survival recovery targets have not been specified for any region of the west coast of North America outside the Columbia River Basin. Within the extensively dammed Columbia River Basin, the Northwest Power and Conservation Council's Fish and Wildlife Program (NPCC) set rebuilding targets for SARs at 2%-6% (McCann et al., 2018, p. 4), roughly the survival observed in the 1960s prior to the completion of the eight-dam Federal Columbia River Power System (FCRPS) (Raymond, 1968, 1979). The NPCC SAR objectives did not specify the points in the life cycle where Chinook smolt and adult numbers should be determined; however, one extensive analysis for Snake River spring/summer Chinook was based on SARs calculated as the proportion of smolts reaching the uppermost dam in the migration path that survived to return there as adults and jacks (Marmorek et al., 1998): "*Median SARs must exceed 4% to achieve complete certainty of meeting the 48-year recovery standard, while … A median of greater than 6% is needed to meet the 24-year survival standard with certainty*" (p. 41). Although not explicitly stated, this seems to be the basis for setting the 2%–6% rebuilding standard for the Columbia River.

In this paper, we collate Chinook SAR time series for the west coast of North America to document broad patterns in survival. The SAR is the threefold product of freshwater smolt survival during downstream migration multiplied by the marine survival experienced over two to three years in the ocean and multiplied by adult freshwater survival during the upstream migration to the final census point. Survival should include animals removed by the fisheries; however, as we show later, harvest is not included in PIT tag-based survival estimates, which has significant implications.

There are two major methods of estimating survival on the west coast of North America, one using coded wire tags (CWT) and another using passive integrated transponder tags (PIT). We assessed whether the SAR estimates using these methods could be pooled for analyses but concluded that they are not interconvertible. The CWT program is more geographically extensive; thus, our primary analysis uses the CWT-based estimates for coast-wide survival comparison. However, within the Columbia River Basin, PIT tags have been widely relied upon for over two decades as the primary source of survival data, so we separately analysed the survival patterns reported using the PIT tag methodology. The collated data are presented by region, smolt age at outmigration, stock, and/or year of outmigration. We then tested the current similarity of SAR estimates across regions using data from the five most recent years of available data. Given the widely recognized poor survival of Snake River Chinook salmon, resulting in their listing under the US Endangered Species Act (NMFS, 2017a, 2017b), many of our analyses compare regional survival to that of the Snake River region. We show that, overall, Chinook salmon survival (SAR) has decreased by roughly the same amount everywhere along the west coast of North America and has now reached similar or lower survival levels than Snake River stocks.

In the process of assessing how well survival estimates from CWT and PIT-based tagging methodologies can be compared, we found that there were large population-specific changes in harvest rates over time which are not incorporated into PIT tag-based survival estimates. This previously unrecognized limitation of PIT tagging methodologies is critical to current conservation efforts in the Columbia River Basin because of changes to the terms of the US-Canada Pacific Salmon Treaty, which we outline.

Finally, we examined the CWT and PIT tag SAR data sets to evaluate the broader evidence for "delayed mortality," an important theory that argues that the greater dam passage experienced by Snake River stocks predisposes these populations to lower subsequent survival after migration out of the hydropower system than populations not migrating through the Snake River dams.

At the broadest level, the major implication of our results is that most of the salmon conservation problem is determined in the ocean by common processes. Attempts to improve SARs by addressing region-specific issues such as freshwater habitat degradation or salmon aquaculture in coastal zones are therefore unlikely to be successful. Given the importance of these conclusions, we call for a joint systematic review by major funding agencies to further assess the broader consistency and comparability of SAR data with our findings.

2 | METHODS

2.1 | Data sources

Most survival rates of Pacific salmon are based on mark-recapture efforts, where juveniles are "marked"—implanted with either coded wire tags (CWT) or passive integrated transponder (PIT) tags—and recaptured in the fishery or detected upon return to the river. CWT technology dates back to the 1960s. A review is provided by Johnson (1990); the application of the methodology to coastal marine migrations of Coho and Chinook is described by Weitkamp (2009) and Weitkamp and Neely (2002) and to measuring harvest and survival by ADF&G Chinook Salmon Research Team (2013), Bernard and Clark (1996), and Chinook Technical Committee (2014). The CWT tag is implanted in the nose cartilage of smolts. If recaptured in the fishery, the fish must be dissected to recover the tag and the tag code must be read with a microscope. In contrast, PIT tags first came into widespread use in the Columbia River Basin in 1997. They are long-lived but short-distance radio-frequency tags that can successfully transmit their unique ID code when within <0.5 m of a detector (Prentice et al., 1990a, 1990b, 1990c; Skalski et al., 1998). The short detection range essentially limits the use of PIT tags to either small, shallow streams or the Columbia River dams, which channel sufficient tagged individuals close to the detectors to generate useful survival estimates.

We collated SAR time series for Chinook from several sources (Table S1). For CWT-based estimates, the primary data are the survival estimates for the indicator stocks used by the Pacific Salmon Commission (PSC). These data sets are formally submitted to the PSC by a wide variety of management agencies under the terms of the bilateral US-Canada Pacific Salmon Treaty. We supplemented these with CWT-based SAR time series published in the primary or secondary literature or calculated directly from the Pacific States Marine Fisheries Commission's CWT database. Together, these data sets represent California, Oregon, Washington, British Columbia, and southeast Alaska. Early SAR estimates for the Upper Columbia and Snake Rivers are based on freeze-branding (Raymond, 1988), but were included because they are the only estimates available for the time period when SARs collapsed in those regions. Finally, because of their historical importance to monitoring in the Columbia River, we compiled and separately analysed the PIT tag-based SAR estimates reported by the Comparative Survival Study (McCann et al., 2018).

Because SAR data are typically log-normally distributed, we primarily report the median, as this is equivalent to the geometric mean some authors use. (A simple proof of this statement is to note that after log-transformation the mean of log-normal data will have 50% of the data above and below it.) We therefore use the simpler terminology both for clarity and because the median is invariant under log-transformation, which is not true for the mean.

2.2 | Pacific Salmon Commission (CWT-based estimates)

The PSC is a bilateral treaty organization between the US and Canada coordinating management of Pacific salmon from Cape Falcon, Oregon, north to Cape Suckling, Alaska. The data are contributed to the Chinook Technical Committee of the PSC by the various government agencies responsible for conducting the individual monitoring programmes. This database was the source of CWT-based Chinook survival estimates for all regions outside the Columbia River Basin and for a few stocks located in the Columbia River Basin.

The PSC database provides several measures of SAR. We used their estimates calculated as the sum of adults returning at all ages or caught in the fisheries, uninflated for losses to natural mortality for Chinook remaining at sea for longer than two years:

$$\mathrm{SAR}_{l,j} = \frac{\sum_{k=2\ \text{or}\ 3}^{\text{max age}} \left(\sum_{i=1}^{n} \left(F_{i,j,k,l} + \mathrm{IM}_{i,j,k,l} \right) + \mathrm{Esc}_{i,j,k} \right)}{\mathrm{Rel}_{i,j}}$$

where $F_{i,j,k,l}$ are the tags recovered in fishery *l*, for age *k*, from brood year *j*, of stock *i* that are expanded for the fraction of the catch sampled; $IM_{i,j,k,l}$= the incidental mortalities; and $Esc_{i,j,k}$= the number of tags recovered in the escapement, including hatchery and spawning ground recoveries, that are expanded for the fraction sampled. Columbia River stocks also have an interdam loss (IDL) calculation, so fish (or tags) returning to the river are adjusted upward to account for in-river mortality (Chinook Technical Committee, 2018).

CWT-based SAR estimates for hatchery-origin fish generally cover the period from hatchery release until adult return to the hatchery and/or spawning grounds and are compensated for harvest (i.e., mortalities due to harvest are included as survivors). Exceptions include five Alaskan hatcheries used in our analysis which are located at sea level and which release smolts directly into the ocean after several weeks of seawater acclimation in holding pens, eliminating losses in freshwater (see later). For wild stocks, juvenile fish are captured and tagged during downstream migration, and therefore, some of the CWT-based survival estimates for wild stocks are biased high because they can exclude survival losses occurring in the initial phase of the migration upstream of the census point (McPherson et al., 2010). Other miscellaneous notes about this data set are recorded as footnotes at the bottom of Table S1.

2.3 | Agency estimates (CWT-based estimates)

The PSC does not include indicator stocks for California or for yearling Chinook from the Columbia River, presumably because these stocks are not relevant to international management. We therefore included published estimates for fall, late-fall, and winter Chinook runs from the Sacramento River in California (Michel, 2018). For Columbia River Basin spring Chinook, we collated some annual reports produced by individual hatcheries in the basin and/or contacted the hatcheries directly to build up a partial inventory of CWT-based SAR estimates for Chinook.

These supplemental estimates were calculated similarly to those done by the PSC but are unexpanded for incidental mortality (or interdam loss in the Columbia River). Hatcheries that do not tag 100% of smolts released may expand their estimates for the proportion tagged while others are estimated using only tagged fish. See Table S1 for details.

2.4 | Pacific States Marine Fisheries Commission estimates

All CWT release and recovery data are submitted to the Regional Mark Processing Center hosted by the Pacific State Marine Fisheries Commission, which maintains the online Regional Mark Information System (RMIS) to facilitate exchange of CWT data. We investigated this source; however, we could not verify that adult return numbers from all possible significant components were correctly incorporated and expanded for sampling effort. Ideally, adult returns should include hatchery rack returns (adults taken for brood stock), adult escapement to spawning grounds, and immature or maturing individuals caught in all fisheries (sport, commercial, tribal) and locations (at sea, in-river). For this reason, we focused on the PSC and Agency estimates described above. We used RMIS only for Entiat Spring Chinook (UCOL) after consulting with Entiat Hatchery biologists on the integrity of the data set (G. Fraser, *pers. comm*. USFWS, Leavenworth, WA. gregory_fraser@fws.gov).

2.5 | Raymond (1988) estimates

Data on survival in the 1960s to early 1980s period for the Snake and Upper Columbia Rivers was based on mark-recapture estimates of the abundance of a mixture of freeze-branded hatchery and wild smolts passing the first dam encountered each year (Raymond, 1988). An essentially complete enumeration of adult returns was possible at upstream dams several years later because the adults must ascend fish ladders and estimates were compensated for harvest. These SAR estimates are inflated relative to the CWT-based estimates described above because they do not include migration losses from the time downstream migration is initiated until the smolts are censused at the dams and also exclude adult upstream losses between the dam and the spawning grounds. Nevertheless, this data set is important because it incorporates the period of relatively high survival in the 1960s and early 1970s and the period when survival collapsed, which was attributed primarily to dam construction. We used these estimates in conjunction with the CWT estimates for a more complete time series.

2.6 | Comparative Survival Study (PIT tag-based estimates)

PIT tags have largely supplanted CWTs in the Columbia River Basin because of the ability to measure smolt survival between dams and estimate SARs. We used the estimates of overall SAR from Chapter 4 of the Fish Passage Center's Comparative Survival Study (McCann et al., 2018) which are essentially the number of adults returning to the uppermost FCRPS dam with detection capability (Lower Granite, McNary, John Day and/or Bonneville dams depending on the population) divided by the estimated number of PIT-tagged smolts surviving to their uppermost dam during downstream migration. For example, for most Chinook salmon originating from the Snake River Basin, the SAR is estimated from Lower Granite Dam back to Lower Granite Dam.

When estimates were available for multiple segments, we selected the SAR covering the greatest extent of the migratory life history (i.e. smolt releases and adult returns to the uppermost dam available in the Columbia River Basin), and we used SAR estimates that included jacks when available. In the mid-Columbia region, SAR estimates with jacks were sometimes available only for a shorter migration segment; in these cases we selected the SAR data sets representing the longer migration segment but excluding jacks because this was most similar to the CWT survival estimates. PIT tag-based SARs do not incorporate losses due to harvest (McCann et al., 2018, p. 95) because the commercial and sport catch is not monitored for PIT tags.

Because PIT tag-based SAR estimates contain several limitations that are problematic to the interpretation of survival (particularly lack of harvest information), we use these estimates only as a secondary validation of the major conclusions.

2.7 | Division by life history

Chinook salmon display two major juvenile life history types (subyearling and yearling) that correspond with adult run-timing (fall or spring, respectively). These life history types are examined separately in our analysis because there are important ecological differences between them (see reviews by Riddell et al. (2018) and Sharma and Quinn (2012)) which likely influence survival. We review the general characteristics below but note that this simple picture is more complicated due to hatchery rearing practices and natural variability.

Subyearling/fall populations are widely distributed in low gradient coastal streams or the lower mainstem of major rivers but are absent from Alaska. They migrate to the ocean within a few months of hatching and almost certainly remain as long-term residents of the continental shelf off the west coast of North America where they are exposed to commercial and sport harvest in coastal marine waters over multiple years (Sharma & Quinn, 2012). Survival of shelf-resident subyearling Chinook populations can therefore be significantly reduced by coastal fisheries that can harvest these animals over several years of marine life.

Yearling/spring populations are found in headwater tributaries of large river systems penetrating well into the interior of the continent, such as the Columbia and Fraser rivers. They migrate to sea after completing one or more full years of life in freshwater and are thus significantly larger at ocean entry. Yearlings (generally) spend one less year in the ocean than subyearlings. Only the yearling life history type is found in Alaska (Healey, 1983).

Yearlings are thought to migrate along the continental shelf as juveniles and then move offshore and become purely open ocean residents for much of the marine phase and thus are essentially immune to harvest by directed salmon fisheries until their return to the shelf and freshwater, where variable levels of harvest may occur. However, significant by-catch of Chinook populations originating from as far away as Washington and Oregon occurs in Alaskan trawl fisheries (Larson et al., 2013), which may possibly include yearling Chinook.

2.8 | Comparisons between regions

To develop a formal statistical test of the similarity in SARs between regions in the most recent years of the record, we first grouped the CWT-based SAR data separately by smolt age (yearling/subyearling), region, and rearing type (hatchery/wild). For each of these groupings, we pooled all data in the 2010–2014 ocean entry period across all populations in a region and then resampled the pooled data with replacement $N = 10{,}000$ times, each time drawing a sample of the same size as the original pooled data. We chose this time period because there was a consistent number of populations contributing to each regional grouping used in the comparison period (2014 being the last year with essentially complete data available for all populations) and it avoided including 2008, a year of unusually cold conditions (Arguez et al., 2020). Limiting the samples to this period ensured the data were current and removed the potential variability due to differing lengths of the time series. For each group, we calculated the N median SARs and then calculated the ratio of those N medians with those from each of the other regions in turn. The empirical distribution of the N ratios allows for a formal statistical test of the proposition that median SARs in two regions are equal (i.e. that the ratios are not different from one). The normalized SAR ratio for region i relative to the Snake River in sample $j = 1,.., N$ was then $SAR_{i,j}/SAR_{SNAK,j}$. Because of the generally recognized poor survival of Snake River Chinook salmon, we present the results of the comparison to the Snake River in the main text but also provide the comparison using all possible regions in the denominator in Figure S1.

2.9 | Comparison between CWT and PIT tag-based SARs

There are some fundamental differences between PIT and CWT tag-based SAR estimates. PIT tag-based SARs exclude smolt and adult survival upstream of the topmost dam where they are censused and do not account for harvest in ocean or mainstem river fisheries. CWT-based estimates incorporate these factors. Therefore, an aggregate correction factor $\widehat{c_{i,j}}$ for the PIT-based SAR estimates to make them consistent with the CWT-based SAR estimates is:

$$\widehat{c_{i,j}} = \frac{S_{i,j}^{smolt} * S_{i,j}^{adult}}{(1 - h_{i,j})}$$

where $S_{i,j}^{smolt}$ is the estimated survival of stock i between the hatchery or presmolt rearing grounds and the uppermost dam for smolts from brood year j; $S_{i,j}^{adult}$ is the estimated survival of stock i between the uppermost dam and return to the hatchery/spawning grounds; and $h_{i,j}$ the estimated harvest of stock i in year j. For simplicity, we neglect harvest in years prior to adult return. Here, the numerator corrects for upwards bias in PIT-based SAR estimates caused by excluding survival above the topmost dam while the denominator corrects for the downward bias caused by excluding harvest.

We were interested in estimating $c_{i,j}$ to assess if it was reasonable to use it to combine these data into a single term that could provide a reliable metric for converting between PIT and CWT-based SAR estimates. To do this, we first attempted to collate the three components ($S_{i,j}^{smolt}$, $S_{i,j}^{adult}$ and $h_{i,j}$) for the populations with PIT tag SAR estimates, but we encountered difficulty obtaining sufficient data, particularly for the adult stage. However, combined ocean plus mainstem harvest rates were readily available for the PSC's indicator stocks. For yearling populations, marine harvest rates are thought to be very low (Waples et al., 2004) and are not included in the CTC database. We therefore collated mainstem harvest data from other sources for yearlings (Table S2).

Our second approach to estimating $c_{i,j}$ was to identify populations with both CWT- and PIT-based SAR estimates generated in the same years and then use simple linear regression to identify the relationship. If there was no difference between estimation methodologies, then the regression of CWT SAR estimates on PIT tag-based SAR estimates should have a regression slope of $\hat{c} = 1$.

3 | RESULTS

We collated 123 eastern North Pacific Ocean Chinook salmon SAR time series totalling 2,279 years of monitoring (Figure 1). SAR estimates included in our analysis were from populations extending from central California to south east Alaska and include 94 hatchery populations, 26 wild, and 3 hatchery-wild (mixed) populations. These populations were then aggregated by geographic area to compare regional SARs. All time series outside the Columbia River watershed are based on CWTs. Within the Columbia, both PIT and CWT-based SARs were available.

3.1 | SARs from coded wire tags

Most regions of west coast North America with CWT time series extending back prior to the 1978 regime shift (Beamish, 1993; Beamish & Bouillon, 1993; Ebbesmeyer et al., 1990; Francis & Hare, 1994; Mantua et al., 1997) show an approximate threefold decrease in SARs for hatchery populations (Figure 2). This applies to hatchery subyearling Chinook from west coast Vancouver

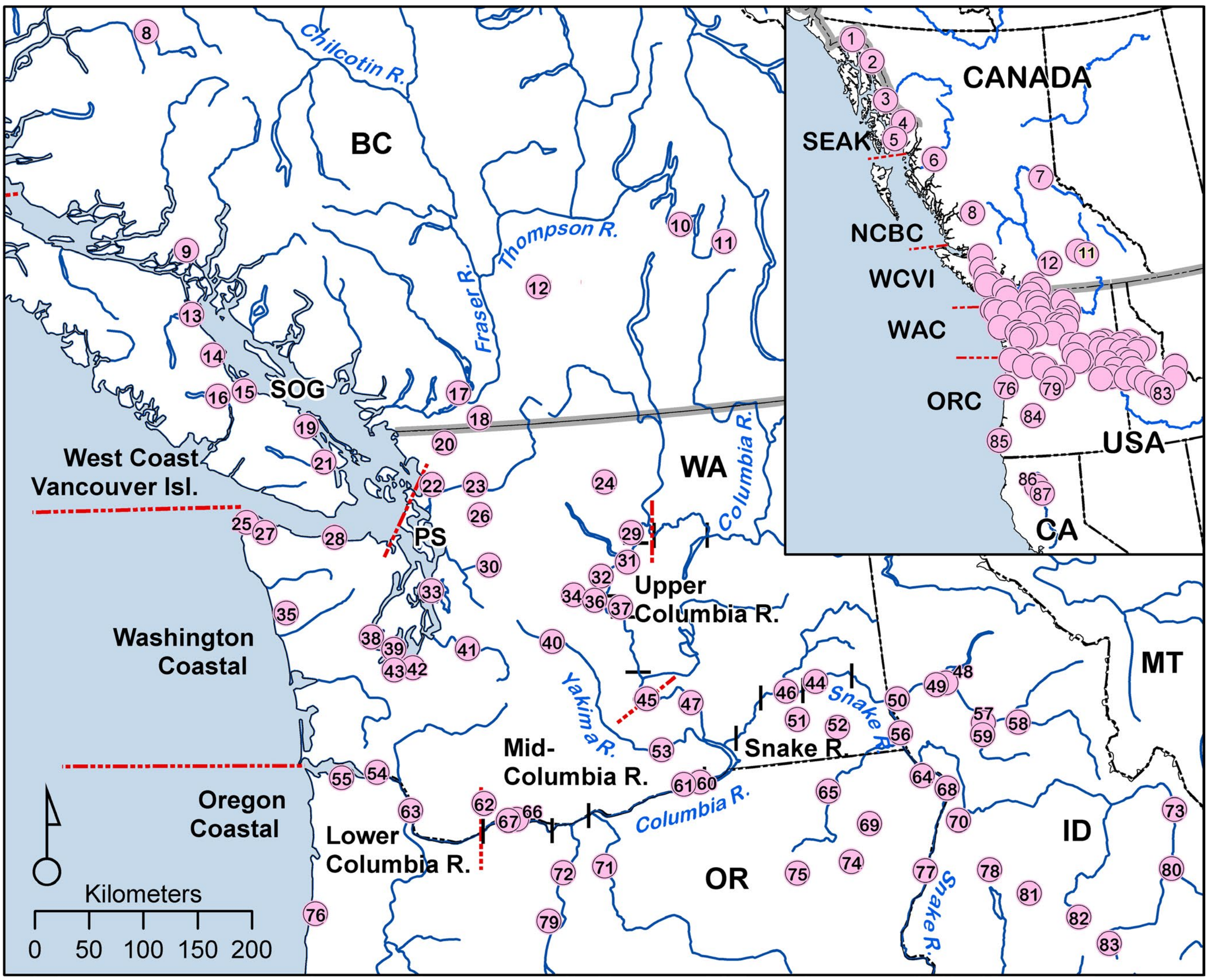


FIGURE 1 Map of the locations of Chinook salmon survival time series used in the analyses. Numbers inside symbols are keyed to the populations in Table S1. SEAK = SE Alaska/Northern British Columbia Transboundary Rivers; NCBC = North-Central British Columbia; WCVI = West Coast Vancouver Island; WAC = Washington Coastal; ORC = Oregon Coastal; SOG = Strait of Georgia; PS = Puget Sound; CA = California. (Figure appears in colour in the online version only)

Island, the Strait of Georgia, Puget Sound, and the mid-Columbia River; and to hatchery yearling Chinook from SE Alaska, the lower and upper Columbia River, and the Snake River (upper Columbia and Snake rivers are relative to the historical freeze brand data from Raymond (1988)). Except for coastal Oregon subyearlings, average CWT-based SARs for hatchery fish for all regions are now approximately 1% or less.

Within the Columbia River Basin, hatchery Chinook from all regions except for yearlings from the lower Columbia show some increase in CWT-based SARs since the 1980s and early 1990s, the period when SARs reached their lowest values in the basin. None of these time series have recovered to the survival levels measured by Raymond (1988) in the 1960s.

Median population-specific SARs show that wild populations generally have higher survival than hatchery populations; however, there are limitations: CWT data are limited for wild populations and there are no data available for a direct hatchery versus wild comparison for the same population (Figure 3). The wild yearling Chinook populations in SE Alaska tend to have lower survival than the hatchery-reared population; however, the Alaskan hatchery SAR estimate provided to the PSC is based on combined data for five hatcheries that all release smolts directly into the ocean after acclimation to seawater for several weeks, eliminating losses from freshwater migration (Bill Gass, Production Manager, Southern Southeast Regional Aquaculture Association, & John Eiler, NOAA; pers. comms.).

Median SARs for hatchery or wild populations within a given region tend to cluster together, but a few populations (University of Washington experimental hatchery releases in Puget Sound and the Chilliwack hatchery in the Strait of Georgia) have unusually high SARs relative to other stocks in their respective region. These are also the only populations whose medians substantively attain the 2%–6% SAR recovery level adopted in the Columbia River Basin. Apart from SE Alaska and north-central BC yearlings and Oregon Coast subyearlings, which have higher regional survivals, populations from other regions have only rarely reached this level of production.

3.2 | Comparison between regions

To compare the current status of regional CWT-based SARs, we included the five most recent years of consistently available SAR data (2010–2014) in a resampling procedure to statistically quantify relative SARs. We used Snake River population SARs as the baseline region to compare all other regions with because of the perceived status of the Snake River as having particularly poor survival; the same analysis using other regions as the basis for comparison is presented in Figure S1. A striking result emerges for hatchery-reared subyearling Chinook: median SARs in all regions except the Oregon Coast are lower than median Snake River SARs (Figure 4). Only in three of nine regions with numerically lower SARs does the upper 5th percentile of the empirical distribution include the possibility of

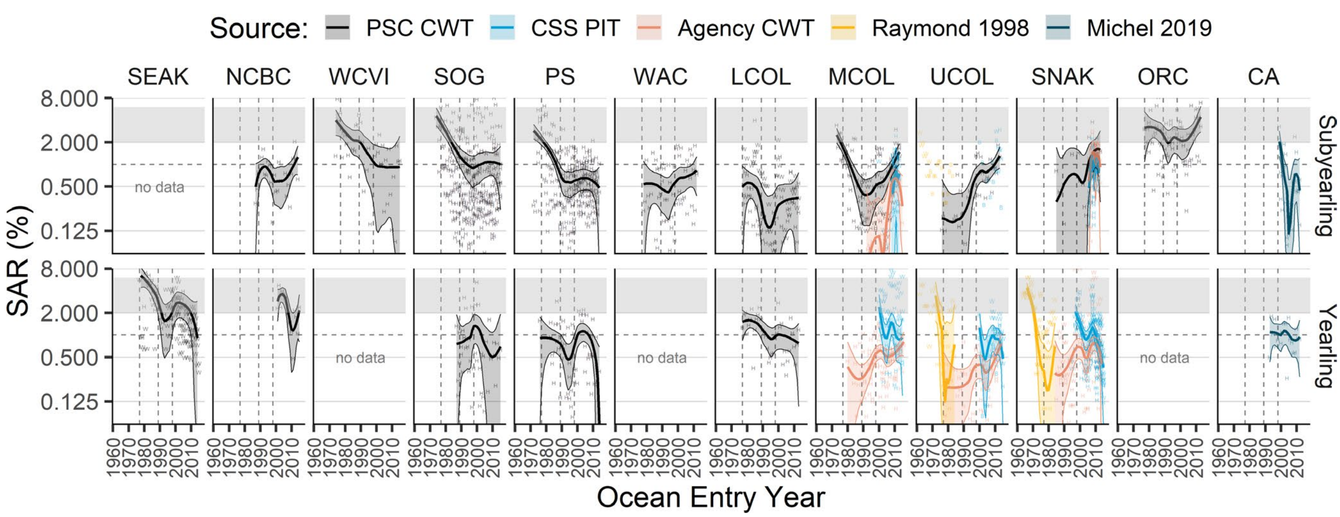


FIGURE 2 Time series of smolt-to-adult return (SAR) estimates for Chinook salmon plotted by source. (The online version of the figure supports substantial magnification to examine the details of each panel.) Annual SAR estimates for hatchery (H), wild (W) and mixed hatchery-wild data sources (B) are shown, but regional loess curves of survival and associated 95% confidence interval use hatchery data only, colour coded by data source. In order to focus on the trends, a few SAR estimates have been clipped by restricting the y-axis maximum to near the loess curve maxima. Blank panels indicate regions where the life history type does not occur. The SAR 2%–6% recovery target adopted for Snake River Spring Chinook is shown as a grey band. The timing of the major regime shifts starting in 1977, 1989 and 1998 are indicated by vertical dotted lines. The horizontal dotted line indicates 1% SAR. Note logarithmic y-axis. Sources correspond to Table S1 as follows: PSC CWT = PSC 2019; CSS PIT = McCann et al., 2018; Agency CWT = all other sources exclusive of Raymond 1998 and Michel 2019. CWT = coded wire tag; CSS = Comparative Survival Study, PIT = Passive Integrated Transponder; SEAK = SE Alaska/Northern British Columbia Transboundary Rivers; NCBC = North-Central British Columbia; WCVI = West Coast Vancouver Island; SOG = Strait of Georgia; PS = Puget Sound; WAC = Washington Coastal; LCOL = Lower Columbia River; MCOL = Mid-Columbia River; UCOL = Upper Columbia River, SNAK = Snake River; ORC = Oregon Coastal; CA = California. (Figure appears in colour in the online version only)

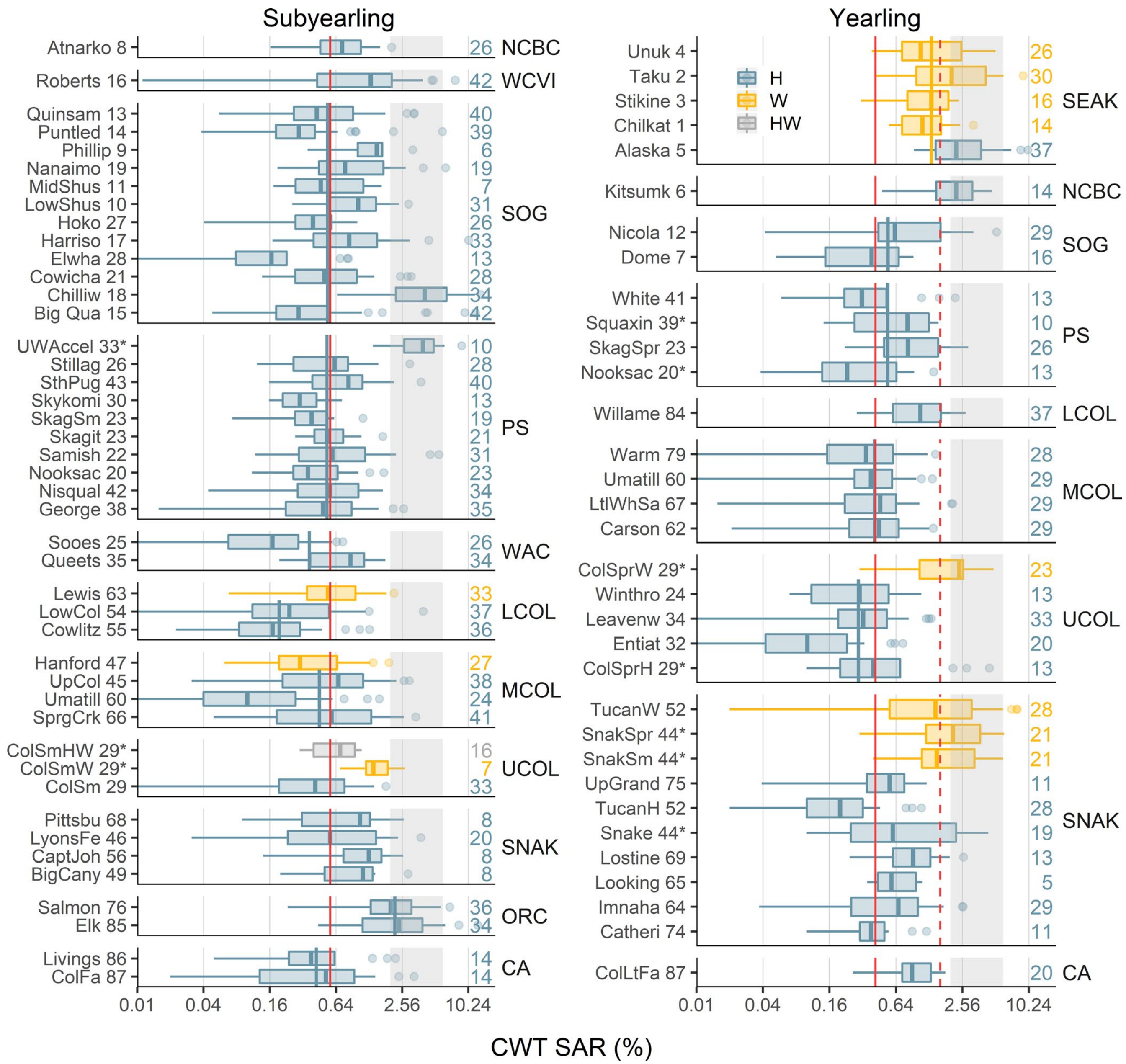


FIGURE 3 Chinook survival (SAR) based on coded wire tags, disaggregated by population and region; all years combined. Central lines show medians, boxes show the interquartile range (central 50% of data points), whiskers bracket 1.5 times the interquartile range, and open circles identify outliers. Regional medians are computed using all populations and shown as vertical blue (hatchery) or gold (wild) lines, with Snake River medians overplotted as vertical red lines on all panels for comparison (H = solid red and W = dashed red). The 2%–6% target recovery range for Snake River SARs is shown as a shaded band. The number of SAR estimates for each population is shown to the right. See Table S1 for definitions of population acronyms and Figure 2 for region acronyms. H = hatchery; W = wild; HW = mixture. *Indicates data sets ending prior to 1998 (all data from Raymond (1998) and three Puget Sound data series from PSC (2019)). (Figure appears in colour in the online version only.)

equal SARs with the Snake River region (North-Central BC, mid and upper Columbia). For all other regions, subyearling SARs are statistically lower than the Snake River survivals. There are no CWT-based SAR estimates for wild subyearling Chinook.

Applying the same procedure to hatchery-reared yearling Chinook, current regional SARs were statistically indistinguishable from Snake River SARs for the Salish Sea (Strait of Georgia, Puget Sound) and all other regions of the Columbia River Basin (Lower, Mid, and Upper; Figure 4). California, northern BC, and SE Alaska yearling SARs were significantly higher than Snake River yearling populations. The SARs of SE Alaska wild yearling Chinook (four river systems) were significantly lower than the SARs of the one wild stock of Snake River yearling Chinook for which we have data (Tucannon River; Figure 3).

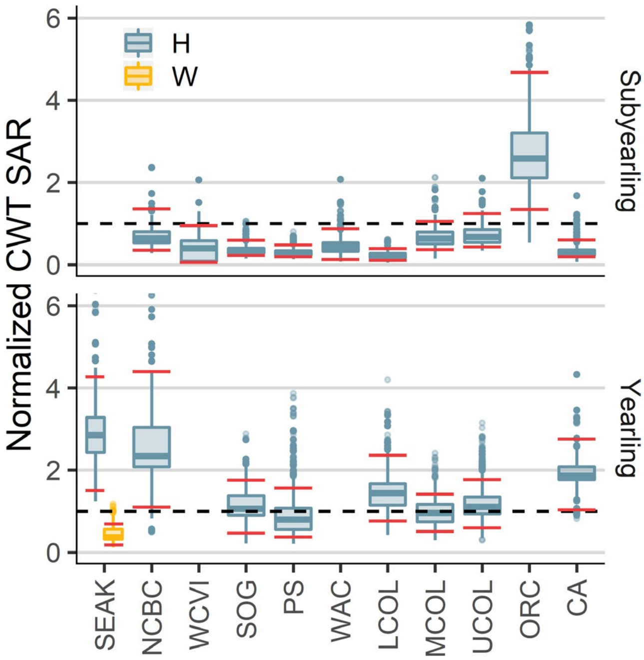


FIGURE 4 Regional CWT-based SAR estimates for Chinook salmon normalized relative to Snake River SARs for the 2010–2014 period. Estimates above the horizontal black dotted line indicate higher survival than Snake River populations. Horizontal red lines show the empirical 5% and 95% percentiles on the sampling distribution of the normalized ratio. See Fig. S1 for SAR estimates normalized to all other regions. H = hatchery; W = wild. (Figure appears in colour in the online version only.)

3.3 | SARs from PIT tags

PIT tag-based SAR estimates are available for Chinook salmon originating from the Columbia River Basin and published annually by the Fish Passage Center (McCann et al., 2018). Comparing PIT tag-based SARs across regions of the Columbia River Basin (Figure 5) yields similar results to the CWT analysis: wild fish generally have higher survival and different regions have similar or lower median SARs to the Snake River. The exceptions are two mid-Columbia populations of wild yearling Chinook salmon (John Day River and Yakima River) which have consistently high SARs that fall within the 2%–6% rebuilding target set for Columbia River Basin yearling Chinook. However, both wild and hatchery subyearling SARs from the mid-Columbia fall well below the Snake River medians, and all other populations (including three hatchery-reared mid-Columbia yearling populations) have SARs which rarely or never exceed 2%; from this perspective only the two wild yearling populations have substantively higher SARs.

3.4 | Comparison of CWT and PIT-based SARs

We attempted to develop a correction factor for PIT tag-based SAR estimates so that we could incorporate PIT-based SAR data sets into our regional comparisons; however, PIT-based estimates differ in two major ways from CWT estimates: (a) they exclude sport, commercial, and indigenous harvest and (b) they exclude smolt and adult losses in the region lying between the uppermost dam and the hatchery or spawning site. Unfortunately, it was difficult to find sufficient comparable data. Where both data types were available for individual populations, regression relationships were strong (high R^2) but biased (greater than or less than the expected 1:1 relationship; Figure 6). Subyearling CWT-based SAR regression estimates were consistently higher than PIT-based estimates (1.3–3.0 times), presumably because the high subyearling harvest rates not captured in PIT-based estimates (currently between ~45%–80%; Figure 7) outweigh the influence of excluding upstream losses. In contrast, CWT-based SAR regression estimates for yearling populations were consistently lower than PIT-based estimates (0.39–0.73 times), indicating that mortality above the uppermost dam outweighs the influence of the generally lower (but not insignificant) harvest rates on yearling populations. Although fitted linear relationships had high R^2, the substantial differences in regression slopes among populations suggest that population-specific factors strongly influence the relationship. A simple correction factor between PIT and CWT-based SAR estimates appears infeasible.

4 | DISCUSSION

4.1 | SAR comparison

Evidence that Chinook salmon survival (SARs) has decreased to roughly 1% in many regions along the west coast of North America is both surprising and important. Direct measurements of SARs are lacking for stocks located west of SE Alaska, but the decrease in the number of adult Chinook returning to the rest of Alaska (ADF&G Chinook Salmon Research Team, 2013; Ohlberger et al., 2016; Schindler et al., 2013) demonstrates that survival has fallen over a very large geographic range.

Although survival data for Asian Chinook salmon populations appear to be lacking, Asian populations have had similarly large decreases in abundance relative to North America, suggesting that the drop in Chinook survival is not restricted only to North America. The reported Asian commercial catch of Chinook averaged just under 10% of the total North Pacific Chinook catch for the 1970–2019 period (NPAFC, 2020). Russian catches for the most recent decade, 2010–2019, were only ¼ of the 1970–1979 average. For Japan, catches in the 2010–2019 period were only 1/60th of the 1970s (NPAFC, 2020). Some of the decrease in Japanese catches is attributable to regulation changes, particularly the 1977 Law of the Sea Treaty which extended coastal state control out to 200 nautical miles (320 km), and resulted in the transfer of harvesting opportunities from Japan to other coastal states. However, the combined Asian catch still declined to only 17% (~1/6th) the level of the 1970s. Thus, although we only have survival data for North American populations, the decline in Chinook abundance due to decreased survival appears to be Pacific basin-wide.

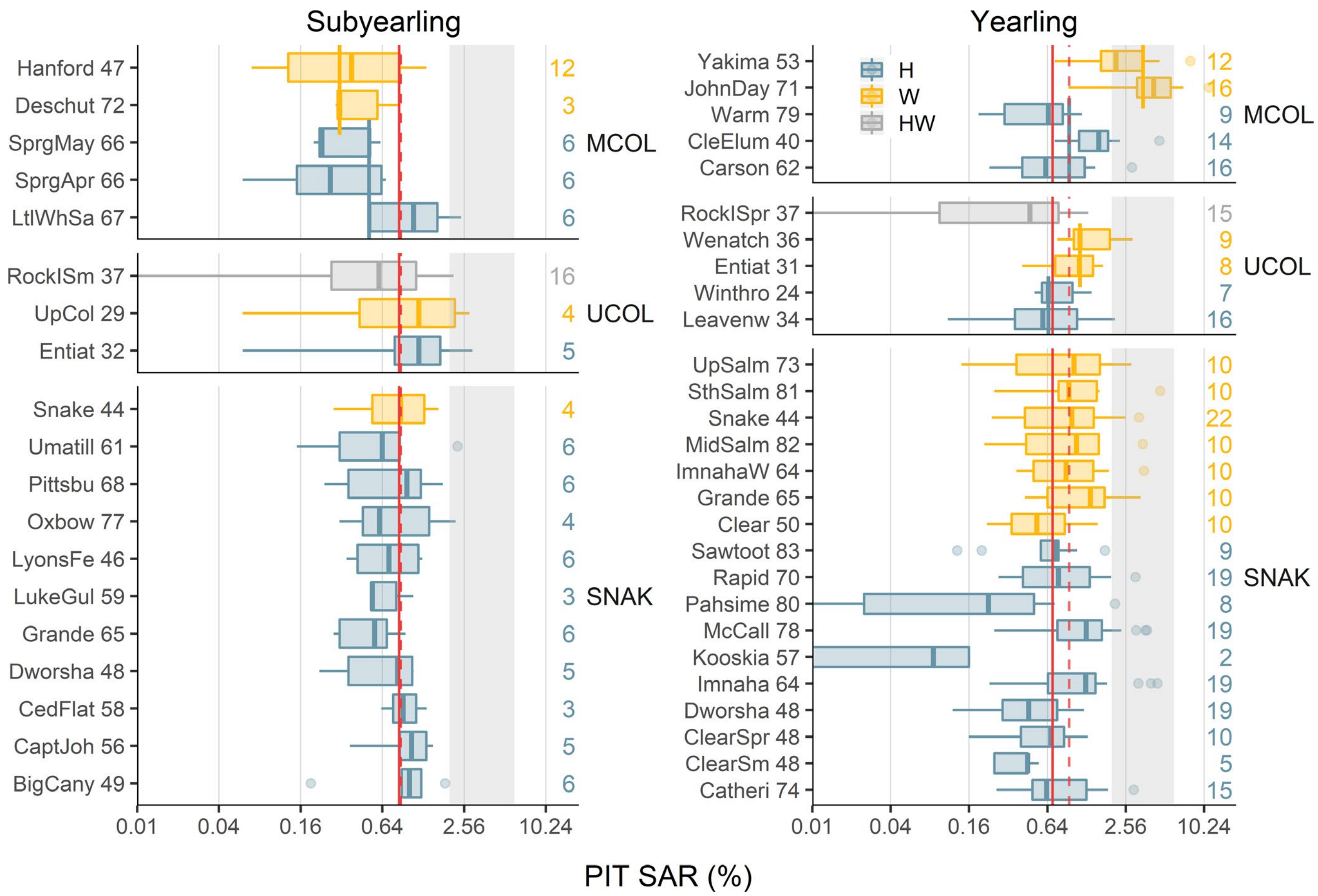


FIGURE 5 Box plots of Chinook PIT tag-based SAR estimates in the Columbia River Basin, disaggregated by population and region; all years combined. These SAR estimates exclude harvest and smolt and adult losses above the topmost dam. Regional medians are computed using all populations and shown as vertical blue (H) or gold (W) lines, with Snake River medians overplotted as vertical red lines on all panels for comparison (H = solid and W = dashed). The 2%–6% target recovery range for Snake River SARs is shown as a shaded band. The number of SAR estimates is shown on the right. H = hatchery; W = wild; HW = mixture. All data from McCann et al. (2018). (Figure appears in colour in the online version only.)

The North American decreases in survival have occurred despite governments' best attempts to increase salmon populations through harvest regulation, hatchery enhancement, and habitat restoration. A major assumption underlying these efforts is that regional factors such as freshwater habitat degradation or salmon aquaculture make important contributions to the decreasing survival of salmon observed coast-wide; however, the similar timing of the decline in the Salish Sea, west coast of Vancouver Island, and Columbia River Basin suggests the primary influence of a broad ocean driver (Beamish, 1993; Beamish & Bouillon, 1993; Mantua et al., 1997). The evidence for a roughly similar drop in Asian Chinook catches reviewed above also indicates that the geographic footprint of any ocean (or freshwater) driver must either be large or that many populations must migrate to common geographic regions where their survival can be similarly reduced.

In the Snake River Basin, where ESA-listed Chinook salmon migrate through eight major dams, subyearling survival of hatchery Chinook is higher than aggregate subyearling SARs from most regions of the west coast of North America, despite the shortness of streams in these other regions and the general absence of dams (Figure 4; Oregon coast is the clear exception). For hatchery-origin yearling populations, the SARs for ESA-listed Snake River populations are lower than those reported for three regions (California, north-central BC and SE Alaska) but are statistically indistinguishable from all other regions (Puget Sound, Strait of Georgia and lower, mid and upper Columbia River).

When comparing wild populations, the few Chinook SAR time series outside of the Columbia River Basin are also not consistently better than wild Snake River SARs, as conventional thinking would assume. The median SAR of four wild Alaskan stocks is slightly lower than the median SAR of three Snake River wild stocks when all years of data are considered (Figure 3) and markedly lower when the comparison is restricted to the 2010–2014 time period (note that the Tucannon River is the only wild population for the Snake River region with recent data; Figure 4). The conclusion is similar when comparing all years of CWT and PIT tag data for most populations (Figures 2, 3 and 5): median SARs are poor everywhere, and generally ~1% except in the earliest years of the time series. Thus, the numerical similarity in SARs is not an artefact of some recent event but something that has persisted for many years. (Tables S3 and S4 provide a summary of the actual numeric values.)

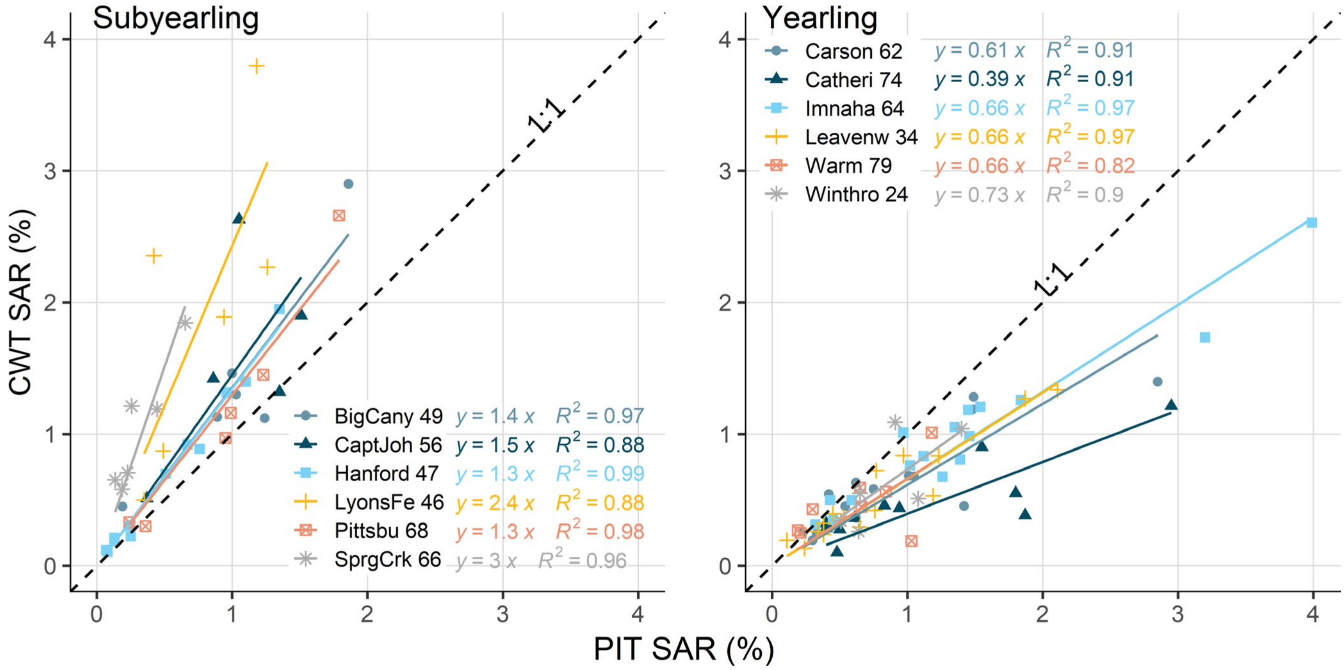
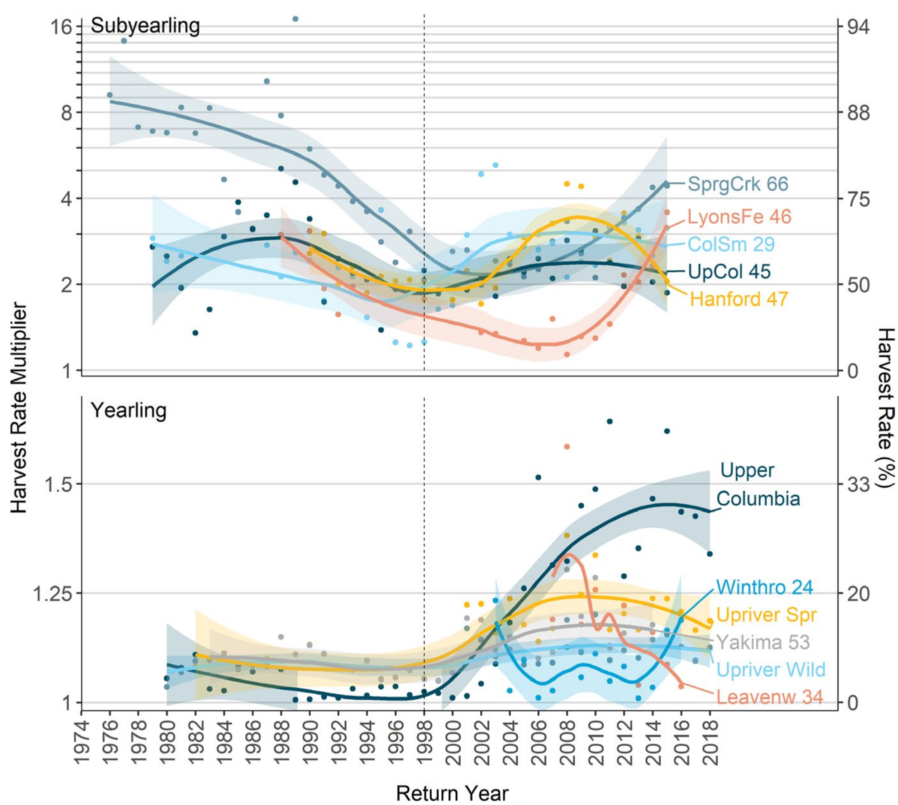


FIGURE 6 Comparison of smolt-to-adult survival (SAR) estimates made using coded wire tags (CWT) and passive integrated transponder (PIT) tags for Chinook salmon populations where both tagging methodologies were employed in the same year. Linear regressions were fit with the intercept constrained to zero. Expanded population names are in Table S1. (Figure appears in colour in the online version only.)

FIGURE 7 Annual Columbia River Chinook harvest rate estimates, fitted loess trend lines, and associated 95% confidence intervals. The right-hand axis shows reported aggregate harvest before Chinook reach McNary Dam. The left-hand axis shows the corresponding value that PIT tag-based SAR estimates should be multiplied by to correct for exclusion of harvest; note log scale. Tributary harvests (i.e. above McNary Dam) are excluded. Substantial variation over time and between populations is evident after 1998 (vertical dashed line), when PIT tag-based survival estimation began. Data sources that present harvest estimates by brood year were converted to return year using the dominant year of return. See Table S2 for population names and references. (Figure appears in colour in the online version only.)



A few populations with anomalously high SARs relative to other populations in the same region exist and provide intriguing evidence that some populations have an intrinsic ability to support higher SARs meeting the Columbia River Basin's current 2%–6% recovery targets (subyearlings from the Chilliwack hatchery in the lower Fraser River (SOG), and a ten-year record of experimental hatchery releases from the University of Washington (PS)). It is unclear why these two populations are more productive. Similarly, a few populations with anomalously low SARs relative to regional medians also are evident (Figure 3). If the underlying reasons for higher or lower survival can be identified it might be possible to improve hatchery productivity more broadly.

Intriguingly, the higher SARs of the two coastal Oregon subyearling populations and Chinook from California (Figures 3 and 4) all involve populations that apparently do not migrate far north. The SARs of California Chinook are particularly noteworthy because freshwater survival is exceedingly low (Michel, 2018); for overall SARS to be higher than Snake River stocks suggests much higher survival during the marine phase. Riddell et al. (2018, p. 580) note the unique marine distributions of southern Oregon Chinook stocks, which restricts them for their entire ocean phase to life in the southern region of the California Current, similar to the assumed ocean distribution of California stocks. It thus seems plausible that specific salmon populations home to distinct feeding grounds, some of which may confer better survival (Quinn et al., 2011; Tucker et al., 2011; Welch et al., 2002).

The reasons for poor marine survival of Chinook are likely multiple, with mechanisms proposed in the last decade alone including: growth (Claiborne et al., 2011; Duffy & Beauchamp, 2011; Graham et al., 2019; Howard, Murphy, Wilson, Moss, & Farley, 2016; Lewis et al., 2015; Losee et al., 2014; MacFarlane, 2010; Miller et al., 2014; Ohlberger et al., 2018; Orsi, 2013; Schindler et al., 2013; Tomaro et al., 2012); hatchery practices (Chamberlin et al., 2011; Nelson et al., 2019; Sabal et al., 2016; Tomaro, 2010); predation (Chasco et al., 2017; Friedman et al., 2019; Miller et al., 2013; Nelson et al., 2019; Seitz et al., 2019); competition (Cunningham et al., 2018; Miller et al., 2013); by-catch mortality in fisheries (Cunningham et al., 2018); and ocean conditions (Dorner et al., 2017; Murphy et al., 2017; Ruff et al., 2017; Sharma et al., 2013).

Delayed mortality, the theory that greater dam passage results in poorer survival of Snake River Spring Chinook relative to mid-Columbia Chinook populations after smolts migrate past the dams (Budy et al., 2002; Independent Scientific Advisory Board (ISAB), 2007; Schaller & Petrosky, 2007; Schaller et al., 1999), is specific to the Columbia River Basin. The theory still plays an important role in Columbia River salmon management (McCann et al., 2019, pp. 116–119); however, direct tests of the theory have not found evidence to support it (ISAB, 2019; Rechisky et al., 2009, 2013, 2014). The PIT and CWT-based SAR estimates assembled here also fail to support the theory because the SARs of Snake River populations are not reduced on average when compared to other regions. Apart from two mid-Columbia wild yearling populations (Yakima River and John Day River) with higher than average survival estimates, all other SAR estimates are similar to Snake River values regardless of differences in the number of dams lying in the migration path. Three PIT-tagged hatchery-reared mid-Columbia yearling populations and two upper Columbia populations have similar SARs to Snake River populations (Figure 5), and CWT-based SAR estimates for lower, mid and upper Columbia yearling populations have survival consistent with Snake River populations (Figure 4). Also of note, both PIT- and CWT-based SAR estimates for Mid-Columbia populations of wild and hatchery subyearling Chinook are generally lower than Snake River values. Thus, none of these comparisons support the claim that greater dam passage—and Snake River dam passage in particular—results in subsequently reduced survival. Our point is not to question that dams cause mortality, but rather to note that their current contribution to reduced survival is likely much smaller than originally believed. We urge biologists to consider all available data when evaluating the delated mortality theory, not just select comparisons that fit the proposed theory.

4.2 | Credibility of SAR estimates

4.2.1 | CWT-based estimates

We restricted most SAR comparisons to CWT-based data, as these are available for the entire west coast to as far north as SE Alaska. Most estimates are for hatchery-reared indicator stocks collated by the Pacific Salmon Commission; few estimates are available for wild populations. For upper Columbia and Snake yearling populations, we used several estimates generated by individual fishery agencies. The PSC cites several challenges with CWT-based estimates including representativeness of the indicator populations, limitations on sampling the fishery and spawning grounds, and distortions introduced by mark-selective fisheries (Hankin et al., 2005). Agencies presumably generate these data using internally consistent methodologies over time to avoid biasing parts of the time series, thus, the large concurrent downward trend in survival of individual populations is likely to be credible.

4.2.2 | PIT tag-based estimates

PIT tag detectors in dam bypasses and fish ladders census both the downstream and upstream movements of PIT-tagged salmon within the Columbia River Basin. Originally developed to study smolt survival, PIT tag-based studies subsequently expanded to measure adult returns, presumably because of the unique ability to completely enumerate returning adults as they ascend fish ladders. SAR data sets are now generated for many yearling and subyearling Chinook populations (McCann et al., 2018) and as a result PIT tags have largely supplanted CWT tags for estimating SARs in the Columbia River Basin. Dividing estimated smolt counts at the dams in the ocean entry year into the returning adult counts in subsequent years provides the SAR.

PIT tag-based SAR estimates show that recent SARs are higher than in the 1980s and 1990s but are generally low compared to historical levels, where available (Figure 2) and track well with CWT-based estimates for individual populations (Figure 6); however, our results indicate that PIT tag-based estimates for Columbia River Basin Chinook are overestimated relative to CWT-based estimates for yearling Chinook and underestimated for subyearling Chinook (Figure 6). Despite being consistent for individual populations, the two methods are therefore not interconvertible. There are two reasons for this. First, for dam-to-dam estimates (e.g. Lower Granite Dam exiting smolts to Lower Granite Dam returning adults), the survival losses incurred upstream of the dam can vary substantially between populations (Faulkner et al., 2017). Unless census points are located at the start and end of the migration period, the amount of excluded upstream survival acts as a population-specific random variable influenced by the excluded distance. This is true for essentially all published PIT-based SAR data (McCann et al., 2018) and for some CWT-based SAR estimates for wild populations, where smolt abundance is censused after migration has started (McPherson et al., 2010).

The second reason is that Chinook harvested in fisheries prior to return are not accounted for in PIT tag-based estimates. Authors have previously noted that PIT tag-based SAR estimates do not include harvest (Marmorek & Peters, 2001; McCann et al., 2018) and recommendations have recently been made to incorporate harvest (ISRP, 2019, p. 22), but neither the magnitude of the harvest nor the variability over time have been recognized. The result is that PIT tag-based SARs represent the surviving adults left over from the operation of multiple fisheries operating over several years. So although PIT tag-based estimates of juvenile survival in the hydrosystem appear reliable, the influence of commercial, sport, and tribal fisheries on adult returns is large, and therefore PIT-based SARs likely do not provide a credible measure of smolt-to-adult survival but rather estimates of escapement from the fisheries to the river.

4.3 | Harvest and PIT-based SARs

The potential of PIT tags to identify all returning adults to the Columbia River is compromised by the inability to identify PIT-tagged fish in the harvest. Ocean harvest rates on Columbia River Basin yearling (Spring) Chinook stocks are ≤2% (Schaller et al., 1999; Waples et al., 2004), presumably because maturing Spring Chinook cross the continental shelf only near their natal river mouth on return and are not exposed to the many coastal fisheries operating along the shelf; however, yearling Chinook harvests in freshwater are still substantial (Figure 7). Harvest rates for Upriver Spring Chinook increased from 10% to 20% of the number arriving at the river mouth over the 1998–2010 period (PFMC, 2019). Not accounting for this river harvest results in underestimating the true SAR by ca. 10% in 1999 (near the beginning of the PIT tag record) and 25% in the more recent years of the record. For other yearling stocks, the correction is larger.

For subyearling Chinook, which are much more heavily harvested, PIT-based SAR estimates likely understate survival by 300%–400% in recent years. For example, Lyons Ferry (Snake River) subyearling Chinook harvest rates rose from a low of ~20% in 2004 to >70% in 2012. These values imply correction factors increasing from 1.25× to >3× over 8 years.

The varying patterns of increase in harvest rates towards the most recent years of the record are particularly important because PIT tag-based SAR estimates do not reflect the higher harvests of recent years and therefore understate the improvements in adult survival that actually occurred. Given the variability in harvest rates over time and between populations, a reliable correction factor to account for harvest will be difficult to achieve for PIT tag-based SAR estimates, while leaving these estimates uncorrected for harvest results in a substantial downwards bias in survival estimates (Figure 6).

Another challenge with using PIT tag-based SAR estimates to set quantitative recovery targets for Columbia River Basin Chinook (e.g., 2%–6% SAR) is that the fisheries management strategy is currently divorced from these goals. Under the terms of the renegotiated Pacific Salmon Treaty, beginning in 1999 coast-wide management of ocean fisheries for Chinook is explicitly abundance-based (Caldwell, 1999; Miller, 2003): fisheries are intensified when abundance is high and restricted when low. Consequently, PIT-based SAR estimates will inaccurately reflect survival if managers identify increases in abundance and increase harvest rates—which is precisely what the treaty dictates they should do. In fact, if managers had perfect control of ocean fisheries survival changes would never be reflected in PIT tag-based SAR estimates because any change in abundance would simply be compensated for by altering harvests. In practice, over or under-harvesting is likely, so PIT-based SAR fluctuations will also reflect the inability to perfectly manage fisheries. Even for Snake River Spring Chinook, where harvest rates are lowest and the interannual fluctuations in harvest are on the order of 10%–20% (Figure 6), survival fluctuations of this size would generally be considered significant. That PIT tag-based SAR fluctuations may simply reflect limitations inherent to the treaty is of concern and appears to be unrecognized. Equally important, expensive changes to the operation of the Federal Columbia River Power System intended to improve survival may benefit the fisheries without credit accruing to those bearing the costs. In future, closer coordination is advisable between the managers implementing abundance-based harvest in the various fisheries and the biologists assessing the impact of Columbia River Basin hydropower operations on survival.

5 | CONCLUSIONS

The policy implications of Chinook salmon SARs falling to about 1/3rd of early levels and converging to similar levels nearly everywhere along the west coast of North America are profound. Current efforts to conserve salmon populations assume that restoring habitats modified by anthropogenic factors (e.g. dams, dykes, forestry, road culverts, salmon farms in the coastal ocean) will improve salmon returns and at least partially compensate for worsening ocean conditions (Roni, 2019). However, if survival also falls by roughly the same amount in regions with nearly pristine freshwater habitats (SE Alaska, north-central British Columbia), it is difficult to argue for a major role of regional factors in causing the decline.

Given the geographically widespread collapse in survival to numerically similar levels and the steadily increasing effort devoted to survival monitoring for salmonids (Figure 8), the fisheries community need to re-assess several core conservation assumptions. Of primary importance is the actual effectiveness of freshwater habitat restoration initiatives when northern populations with nearly pristine freshwater conditions have similar SARs. The resulting policy questions range from the prospect of successfully feeding killer whales with increased hatchery Chinook production, the hypothesized suppressive effect of salmon aquaculture (salmon farming) on wild salmon stocks, to the real role of dams in the demise of endangered Snake River salmon stocks.

As declining survival has reduced adult return rates, there has been mounting effort to increase monitoring. However, we encountered substantial challenges in fully understanding whether all components of adult returns were adequately included in many SAR time series. In addition, some survival time series exclude variable proportions of upstream survival for both smolts and adults. Unless smolt counts are taken at the hatchery (or at the initiation of migration for wild smolts) and adult counts occur on the spawning grounds, variability is introduced into survival estimates because different amounts of the migratory life history are incorporated for different populations. Exactly where abundance is estimated during migration and what components of adult returns are included should be more carefully documented. A coast-wide review of the quality and consistency of smolt-to-adult survival methodologies is needed to ensure that the many initiatives now monitoring survival are achieving sufficient accuracy to be useful.

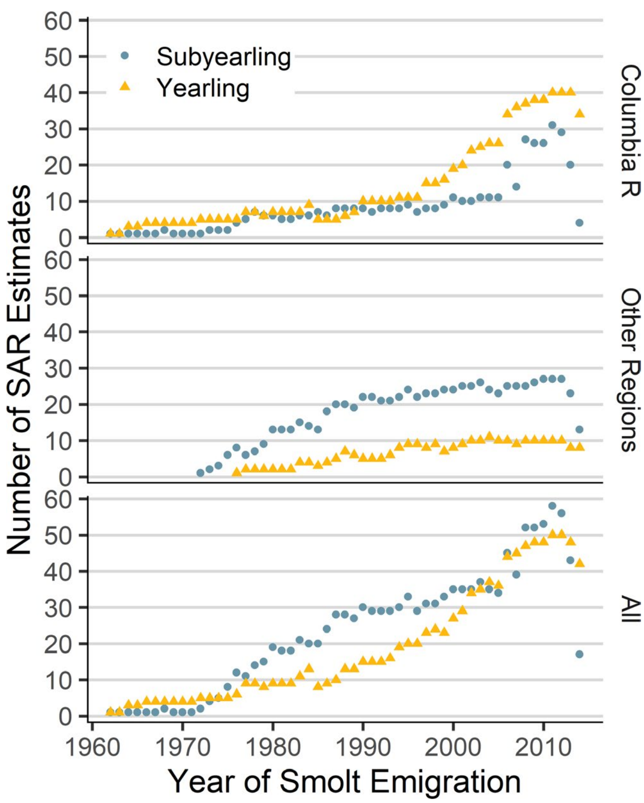


FIGURE 8 Increase in the number of annual SAR estimates used in this paper. The drop in monitoring evident in the most recent years probably reflects lags in data processing rather than a decrease in effort. See Table S1 for specific populations included. (Figure appears in colour in the online version only)

Because of poor survival, the costs of hatchery supplementation are now extremely high. In Puget Sound, where the reported survival of subyearling (Fall) Chinook has fallen to significantly lower survival levels than the Snake River, the cost of hatchery operations to yield one sport-caught adult Chinook has increased from ~$55 (USD) per fish in the 1970s to $768 (yearlings) and $392 (subyearlings) in the 1990s (table 5 of Anonymous (2010); costs unadjusted for inflation). High costs of production are also noted in British Columbia, particularly for Upper Fraser River Chinook, where costs were estimated at $380 (CDN) per returning adult in the 1980s (Winton & Hilborn, 1994). Given the similarity of the decline in survival, the economics of hatchery Chinook production are likely similar in other regions. Understanding the real drivers of poor survival might substantially improve the economics of hatchery production. The few regional hatchery programmes with anomalously high SARs should be investigated to determine when in the postrelease life history period survival is high as a first step to understanding why it is low elsewhere.

It is also important to more carefully consider the role of harvest. Harvest levels for some yearling populations are a considerable fraction of adult returns to the river, while for subyearling populations they are substantially larger than adult escapement. A key part of the renegotiation of the terms of the bilateral US-Canada Pacific Salmon Treaty in 1999 was securing coast-wide agreement that managers would modify harvest in response to abundance. Unfortunately, what went unrecognized was the effect on the many Columbia River studies based on PIT tags. It is unclear whether the quality of reported harvest rate estimates is good enough for past PIT-based SAR estimates to be reliably converted into useful survival estimates. This is an important point because the basic ecological models used to inform the Environmental Impact Statements (EIS) for many ESA-listed Columbia River salmon stocks are calibrated using PIT tag-based SAR estimates (McCann et al., 2018; Zabel et al., 2008). The use of modern parentage-based genetic stock ID methods (Beacham et al., 2020; Freshwater et al., 2016; Hess et al., 2011; Matala et al., 2011; Satterthwaite et al., 2014) may allow apportioning harvest from the various fisheries to source populations with sufficient precision to be useful for survival analysis in the Columbia in the future. However, whether these methods can provide sufficient resolution for past harvest rate estimates to be incorporated into SAR estimate is unclear.

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DATA AVAILABILITY

All data used in the analysis are available without limitation from the Dryad open-access repository (https://doi.org/10.5061/dryad.w6m905qmm).

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REFERENCES

ADF&G Chinook Salmon Research Team (2013). *Chinook Salmon Stock Assessment and Research Plan, 2013* (pp. 56). Retrieved from http://www.adfg.alaska.gov/static/home/news/hottopics/pdfs/chinook_research_plan.pdf

Allendorf, F. W., Bayles, D., Bottom, D. L., Currens, K. P., Frissell, C. A., Hankin, D., & Williams, T. H. (1997). Prioritizing Pacific Salmon stocks for conservation. *Conservation Biology*, *11–1*, 140–152.

Anonymous. (2010). Department of Fish & Wildlife Delayed-Release Chinook Salmon. (Report No. 1003365). State Auditor's Office, State of Washington.

Arguez, A., Hurley, S., Inamdar, A., Mahoney, L., Sanchez-Lugo, A., & Yang, L. (2020). Should we expect each year in the next decade (2019–2028) to be ranked among the top 10 warmest years globally? *Bulletin of the American Meteorological Society*, null. https://doi.org/10.1175/bams-d-19-0215.1

Beacham, T. D., Wallace, C., Jonsen, K., McIntosh, B., Candy, J. R., Willis, D., Lynch, C., & Withler, R. E. (2020). Insights on the concept of indicator populations derived from parentage-based tagging in a large-scale coho salmon application in British Columbia, Canada. *Ecology and Evolution*, *10*(13), 6461–6476. https://doi.org/10.1002/ece3.6383

Beamish, R. J. (1993). Climate and exceptional fish production off the west coast of North America. *Canadian Journal of Fisheries and Aquatic Sciences*, *50*, 2270–2291. https://doi.org/10.1139/f93-252

Beamish, R. J., & Bouillon, D. R. (1993). Pacific salmon production trends in relation to climate. *Canadian Journal of Fisheries and Aquatic Sciences*, *50*, 1002–1016. https://doi.org/10.1139/f93-116

Bernard, D. R., & Clark, J. E. (1996). Estimating salmon harvest with coded-wire tags. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(10), 2323–2332. https://doi.org/10.1139/f96-182

Bradford, M. J., von Finster, A., & Milligan, P. A. (2009). Freshwater life history, habitat, and the production of Chinook Salmon from the upper Yukon basin. *American Fisheries Society Symposium*, *70*, 1–20.

Budy, P., Thiede, G. P., Bouwes, N., Petrosky, C. E., & Schaller, H. (2002). Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. *North American Journal of Fisheries Management*, *22*, 35–51. https://doi.org/10.1577/1548-8675(2002)022<0035:ELDMOS>2.0.CO;2

Caldwell, B. M. (1999). The Pacific salmon treaty: A brief truce in the Canada/U.S. Pacific Salmon War. *The Advocate*, *57*, 379–400.

Chamberlin, J. W., Essington, T. E., Ferguson, J. W., & Quinn, T. P. (2011). The influence of hatchery rearing practices on salmon migratory behavior: Is the tendency of Chinook salmon to remain within Puget Sound affected by size and date of release? *Transactions of the American Fisheries Society*, *140*(5), 1398–1408. https://doi.org/10.1080/00028487.2011.623993

Chasco, B. E., Kaplan, I. C., Thomas, A. C., Acevedo-Gutiérrez, A., Noren, D. P., Ford, M. J., Hanson, M. B., Scordino, J. J., Jeffries, S. J., Marshall, K. N., Shelton, A. O., Matkin, C., Burke, B. J., & Ward, E. J. (2017). Competing tradeoffs between increasing marine mammal predation and fisheries harvest of Chinook salmon. *Scientific Reports*, *7*(1), 15439. https://doi.org/10.1038/s41598-017-14984-8

Chinook Technical Committee. (2014). 2014 Exploitation Rate Analysis and Model Calibration. Volume One. TCCHINOOK (15)-1 V. 1. : Pacific Salmon Commission, Joint Chinook Technical Committee. Retrieved from http://www.psc.org/download/35/chinook-technical-committee/2132/tcchinook15-1_v1.pdf

Chinook Technical Committee. (2018). Joint Chinook Technical Committee Report Annual Report Of Catch And Escapement For 2017. Vancouver: Pacific Salmon Commission Report TCCHINOOK (18)-02.

Claiborne, A. M., Fisher, J. P., Hayes, S. A., & Emmett, R. L. (2011). Size at release, size-selective mortality, and age of maturity of Willamette River Hatchery Yearling Chinook Salmon. *Transactions of the American Fisheries Society*, *140*(4), 1135–1144. https://doi.org/10.1080/00028487.2011.607050

Cohen, B. I. (2012). Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River (Canada). Final Report. Ottawa, Canada: Public Works and Government Services Canada Retrieved from http://epe.lac-bac.gc.ca/100/206/301/pco-bcp/commissions/cohen/cohen_commission/LOCALHOS/INDEX.HTM

COSEWIC (2017). *Assessment and Status Report on the Sockeye Salmon* Oncorhynchus nerka, *24 Designatable Units in the Fraser River Drainage Basin, in Canada*. Committee on the. Status of Endangered Wildlife in Canada. Retrieved from http://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/srSockeyeSalmon2017e.pdf

Cunningham, C. J., Westley, P. A. H., & Adkison, M. D. (2018). Signals of large scale climate drivers, hatchery enhancement, and marine factors in Yukon River Chinook salmon survival revealed with a Bayesian life history model. *Global Change Biology*, *24*(9), 4399–4416. https://doi.org/10.1111/gcb.14315

Dorner, B., Catalano, M. J., & Peterman, R. M. (2017). Spatial and temporal patterns of covariation in productivity of Chinook salmon populations of the Northeastern Pacific. *Canadian Journal of Fisheries and Aquatic Sciences*. https://doi.org/10.1139/cjfas-2017-0197

Duffy, E. J., & Beauchamp, D. A. (2011). Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*, 232–240. https://doi.org/10.1139/F10-144

Ebbesmeyer, C. C., Cayan, D. R., McLain, D. R., Nichols, F. H., Peterson, D. H., & Redmond, K. T. (1990). 1976 step in the Pacific climate: Forty environmental changes between 1968–1975 and 1977–1984. In J. L. Betancourt, & V. L. Tharp (Eds.), *Proceedings of the Seventh Annual Pacific Climate (PACLIM) Workshop (Calif. Dept. of Water Resources*. Interagency Ecological Studies Program Tech. Rept. 26 ed., pp. 115–126).

Faulkner, J. R., Widener, D. L., Smith, S. G., Marsh, T. M., & Zabel, R. W. (2017). *Survival Estimates for the Passage of Spring-Migrating Juvenile Salmonids through Snake and Columbia River Dams and Reservoirs, 2016*. NOAA. Retrieved from https://www.nwfsc.noaa.gov/assets/26/9108_04282017_154932_Spring-Survival-2016.pdf

Francis, R. C., & Hare, S. R. (1994). Decadal-scale regime shifts in the large marine ecosystems of the north-east Pacific: A case for historical science. *Fisheries Oceanography*, *3*, 279–291. https://doi.org/10.1111/j.1365-2419.1994.tb00105.x

Freshwater, C., Trudel, M., Beacham, T. D., Godbout, L., Neville, C.-E., Tucker, S., & Juanes, F. (2016). Disentangling individual- and population-scale processes within a latitudinal size-gradient in Sockeye Salmon. *Canadian Journal of Fisheries and Aquatic Sciences*. https://doi.org/10.1139/cjfas-2015-0344

Friedman, W. R., Martin, B. T., Wells, B. K., Warzybok, P., Michel, C. J., Danner, E. M., & Lindley, S. T. (2019). Modeling composite effects of marine and freshwater processes on migratory species. *Ecosphere*, *10*(7), 1–21. https://doi.org/10.1002/ecs2.2743

Graham, C. J., Sutton, T. M., Adkison, M. D., McPhee, M. V., & Richards, P. J. (2019). Evaluation of growth, survival, and recruitment of Chinook Salmon in Southeast Alaska Rivers. *Transactions of the American Fisheries Society*. *148*, 243–259. https://doi.org/10.1002/tafs.10148

Hankin, D. G., Clark, J. H., Deriso, R. B., Garza, J. C., Morishima, G. S., Riddell, B. E., & Scott, J. B. (2005). *Report of the expert panel on the future of the coded wire tag recovery program for Pacific salmon*. Pacific Salmon Commission. Retrieved from https://www.psc.org/publications/workshop-reports/coded-wire-tag-program-review/

Hare, S. R., Mantua, N. J., & Francis, R. C. (1999). Inverse Production Regimes: Alaska and West Coast Pacific Salmon. *Fisheries*, *24*, 6–14. https://doi.org/10.1577/1548-8446(1999)024<0006:IPR>2.0.CO;2

Healey, M. C. (1983). Coastwide distribution and ocean migration patterns of stream-and ocean-type Chinook Salmon, *Oncorhynchus tshawytscha*. *Canadian Field Naturalist*, *97*(4), 427–433.

Hess, J. E., Matala, A. P., & Narum, S. R. (2011). Comparison of SNPs and microsatellites for fine-scale application of genetic stock identification of Chinook salmon in the Columbia River Basin. *Molecular Ecology Resources*, *11*(Suppl. 1), 137–149. https://doi.org/10.1111/j.1755-0998.2010.02958.x

Howard, K. G., Murphy, J. M., Wilson, L. I., Moss, J. H., & Farley Jr, E. V. (2016). Size-selective mortality of Chinook salmon in relation to body energy after the first summer in nearshore marine habitats. *North Pacific Anadromous Fish Commission Bulletin*, *6*, 1–11. https://doi.org/10.23849/npafcb6/1.11

Independent Scientific Advisory Board (ISAB). (2007). Latent Mortality Report. Review of Hypotheses and Causative Factors Contributing to Latent Mortality and their Likely Relevance to the "Below Bonneville" Component of the COMPASS Model. (Document No. ISAB 2007–1). Retrieved from Portland, Oregon. www.nwcouncil.org/library/isab/isab2007-1.pdf

Irvine, J. R., Fukuwaka, M., Kaga, T., Park, J. H., Seong, K. B., Kang, S., Volk, E. (2009). Pacific Salmon Status and Abundance Trends. : NPAFC Doc. 1199, Rev. 1. 153 pp. Retrieved from http://www.npafc.org/new/publications/Documents/PDF%202009/1199(Rev1)(WGSA).pdf

ISAB (2019). *Review of the Comparative Survival Study (CSS) Draft 2019 Annual Report*. Northwest Power and Conservation Council. Retrieved from https://www.nwcouncil.org/sites/default/files/ISAB%202018-4%20ReviewCSSdraft2018AnnualReport18Oct.pdf

ISRP (2019). *Mainstem and Program Support Category Review*. Northwest Power and Conservation Council, Independent Scientific Review Panel.

Johnson, J. K. (1990). Regional overview of coded wire tagging of anadromous salmon and steelhead in northwest America. Paper presented at the American Fisheries Society Symposium.

Kendall, N. W., Marston, G. W., & Klungle, M. M. (2017). Declining patterns of Pacific Northwest steelhead trout (*Oncorhynchus mykiss*) adult abundance and smolt survival in the ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*, 1275–1290. https://doi.org/10.1139/cjfas-2016-0486

Larson, W. A., Utter, F. M., Myers, K. W., Templin, W. D., Seeb, J. E., Guthrie Iii, C. M., & Seeb, L. W. (2013). Single-nucleotide polymorphisms reveal distribution and migration of Chinook salmon (*Oncorhynchus tshawytscha*) in the Bering Sea and North Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(1), 128–141. https://doi.org/10.1139/cjfas-2012-0233

Lewis, B., Grant, W. S., Brenner, R. E., & Hamazaki, T. (2015). Changes in size and Age of Chinook Salmon *Oncorhynchus tshawytscha* returning to Alaska. *PLoS ONE*, *10*(6), e0130184. https://doi.org/10.1371/journal.pone.0130184

Logerwell, E. A., Mantua, N., Lawson, P. W., Francis, R. C., & Agostini, V. N. (2003). Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. *Fisheries Oceanography*, *12*, 554–568. https://doi.org/10.1046/j.1365-2419.2003.00238.x

Losee, J. P., Miller, J. A., Peterson, W. T., Teel, D. J., & Jacobson, K. C. (2014). Influence of ocean ecosystem variation on trophic interactions and survival of juvenile coho and Chinook salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(11), 1747–1757. https://doi.org/10.1139/cjfas-2014-0043

MacFarlane, R. B. (2010). Energy dynamics and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from the Central Valley of California during the estuarine phase and first ocean year. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*, 1549–1565. https://doi.org/10.1139/F10-080

Mantua, N. J., & Hare, S. R. (2002). The Pacific Decadal Oscillation. *Journal of Oceanography*, *58*(1), 35–44. https://doi.org/10.1023/A:1015820616384

Mantua, N. J., Hare, S. J., 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. .

Marmorek, D., & Peters, C. N. (2001). Finding a PATH toward scientific collaboration: Insights from the Columbia River Basin. *Conservation Ecology*, *5*(2).

D. Marmorek, C. N. Peters, & I. Parnell (Eds.). (1998). Path Final Report For Fiscal Year 1998. (Available from Bonneville Power Administration, Portland, Oregon http://www.efw.bpa.gov/Environment/PATH/reports/ISRP1999CD/PATH%20Reports/WOE_Report/). Compiled and edited by ESSA Technologies Ltd, Vancouver, B.C

Matala, A. P., Hess, J. E., & Narum, S. R. (2011). Resolving adaptive and demographic divergence among Chinook Salmon populations in the Columbia River Basin. *Transactions of the American Fisheries Society*, *140*(3), 783–807. https://doi.org/10.1080/00028487.2011.588092

McCann, J., Chockley, B., Cooper, E., Hsu, B., Schaller, H., Haeseker, S., … Rawding, D. (2018). *Comparative Survival Study of PIT-tagged Spring/Summer/Fall Chinook, Summer Steelhead, and Sockeye*. 2018 Annual Report. Portland, Oregon. Retrieved from http://www.fpc.org/documents/CSS/2018%20CSS%20Annual%20Report.pdf

McCann, J., Chockley, B., Cooper, E., Hsu, B., Schaller, H., Haeseker, S., Rawding, D. (2019). Comparative Survival Study of PIT-tagged Spring/Summer/Fall Chinook, Summer Steelhead, and Sockeye. 2019 Annual Report. Portland, Oregon: Fish Passage Center Retrieved from http://www.fpc.org/documents/CSS/2019CSS_FullDRAFT.pdf

McPherson, S. A., Jones, E. L., Fleischman, S. J., & Boyce, I. M. (2010). Optimal Production of Chinook Salmon from the Taku River Through the 2001 Year Class. Alaska Department of Fish and Game, Fishery Manuscript Series No. 10-03, Anchorage. Retrieved from http://www.adfg.alaska.gov/FedAidPDFs/FMS10-03.pdf

Michel, C. (2018). Decoupling outmigration from marine survival indicates outsized influence of streamflow on cohort success for California's Central Valley Chinook salmon populations. *Canadian Journal of Fisheries and Aquatic Sciences*. 1398–1410. https://doi.org/10.1139/cjfas-2018-0140

Miller, J. A., Teel, D. J., Baptista, A. M., & Morgan, C. A. (2013). Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(4), 617–629. https://doi.org/10.1139/cjfas-2012-0354

Miller, J. A., Teel, D. J., Peterson, W. T., & Baptista, A. M. (2014). Assessing the relative importance of local and regional processes on the survival of a threatened Salmon population. *PLoS ONE*, *9*(6), e99814. https://doi.org/10.1371/journal.pone.0099814

Miller, K. (2003). North American Pacific Salmon: A Case Of Fragile Cooperation Papers Presented at the Norway-FAO Expert Consultation on the Management of Shared Fish Stocks (Vol. FAO

Fisheries Report No. 695, Supplement, FIPP/R695 (Suppl.)). Bergen, Norway, 7–10 October 2002: FAO.

Murphy, J. M., Howard, K. G., Gann, J. C., Cieciel, K. C., Templin, W. D., & Guthrie, C. M. III (2017). Juvenile Chinook salmon abundance in the northern Bering Sea: Implications for future returns and fisheries in the Yukon River. *Deep Sea Research Part II: Topical Studies in Oceanography*, *135*, 156–167. https://doi.org/10.1016/j.dsr2.2016.06.002

Nehlsen, W., Williams, J. E., & Lichatowich, J. A. (1991). Pacific Salmon at the Crossroads: Stocks at Risk from California, Oregon, Idaho, and Washington. *Fisheries*, *16*(2), 4–21. https://doi.org/10.1577/1548-8446(1991)016<0004:PSATCS>2.0.CO;2

Nelson, B. W., Shelton, A. O., Anderson, J. H., Ford, M. J., & Ward, E. J. (2019). Ecological implications of changing hatchery practices for Chinook salmon in the Salish Sea. *Ecosphere*, *10*(11), 1–19. https://doi.org/10.1002/ecs2.2922

Nelson, B. W., Walters, C. J., Trites, A. W., & McAllister, M. K. (2019). Wild Chinook salmon productivity is negatively related to seal density, and not related to hatchery releases in the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(3), 447–462. https://doi.org/10.1139/cjfas-2017-0481

NMFS (2017a). *ESA Recovery Plan for Snake River Fall Chinook Salmon (*Oncorhynchus tshawytscha*)*. National. Marine Fisheries Service. Retrieved from http://www.westcoast.fisheries.noaa.gov/protected_species/salmon_steelhead/recovery_planning_and_implementation/snake_river/snake_river_fall_chinook_recovery_plan.html

NMFS (2017b). *ESA Recovery Plan for Snake River Spring/Summer Chinook (Oncorhynchus tshawytscha) & Snake River Steelhead (Oncorhynchus mykiss)*. National Marine Fisheries Service. Retrieved from https://www.fisheries.noaa.gov/resource/document/recovery-plan-snake-river-spring-summer-chinook-salmon-and-snake-river-basin

Ohlberger, J., Scheuerell, M. D., & Schindler, D. E. (2016). Population coherence and environmental impacts across spatial scales: A case study of Chinook salmon. *Ecosphere*, *7*(4), e01333.

Ohlberger, J., Ward, E. J., Schindler, D. E., & Lewis, B. (2018). Demographic changes in Chinook salmon across the Northeast Pacific Ocean. *Fish and Fisheries*, *9*, 533–546. https://doi.org/10.1111/faf.12272

Orsi, J. (2013). The Alaska Chinook Salmon Production Enigma... What's Going On? *ONCORHYNCHUS.*, *XXXIII*(2), 1–5. Retrieved from http://www.afs-alaska.org/wp-content/uploads/Onco332.pdf

Peterman, R. M., & Dorner, B. (2012). A widespread decrease in productivity of sockeye salmon (*Oncorhynchus nerka*) populations in western North America. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*, 1255–1260.

PFMC (2019). *Review of 2018 Ocean Salmon Fisheries. Pacific Fishery Management Council*. Retrieved from https://www.pcouncil.org/wp-content/uploads/2019/02/2018_Review_of_Ocean_Salmon_Fisheries_Final_021419.pdf

Prentice, E. F., Flagg, T. A., & McCutcheon, C. S. (1990a). Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *American Fisheries Society Symposium*, *7*, 317–322.

Prentice, E. F., Flagg, T. A., McCutcheon, C. S., & Brastow, D. F. (1990b). PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. *American Fisheries Society Symposium*, *7*, 323–334.

Prentice, E. F., Flagg, T. A., McCutcheon, C. S., Brastow, D. F., & Cross, D. C. (1990c). Equipment, methods, and an automated data-entry station for PIT tagging. *American Fisheries Society Symposium*, *7*, 335–340.

Quinn, T. P., Chamberlain, J., & Banks, E. (2011). Experimental evidence of population-specific marine spatial distributions of Chinook salmon, *Oncorhynchus tshawytscha*. *Environmental Biology of Fishes*, *92*(3), 313–322. https://doi.org/10.1007/s10641-011-9841-z

Rand, P. S., Goslin, M., Gross, M. R., Irvine, J. R., Augerot, X., McHugh, P. A., & Bugaev, V. F. (2012). Global Assessment of Extinction Risk to Populations of Sockeye Salmon, *Oncorhynchus nerka*. *Plos ONE*, *7*(4), e34065. https://doi.org/10.1371/journal.pone.0034065

Raymond, H. L. (1968). Migration rates of yearling chinook salmon in relation to flows and impoundments in the Columbia and Snake Rivers. *Transactions of the American Fisheries Society*, *97*(4), 356–359. https://doi.org/10.1577/1548-8659(1968)97[356:MROYCS]2.0.CO;2

Raymond, H. L. (1979). Effects of Dams and Impoundments on Migrations of Juvenile Chinook Salmon and Steelhead from the Snake River, 1966 to 1975. *Transactions of the American Fisheries Society*, *108*(6), 505–529. https://doi.org/10.1577/1548-8659(1979)108<505:EODAIO>2.0.CO;2

Raymond, H. L. (1988). Effects of Hydroelectric Development and Fisheries Enhancement on Spring and Summer Chinook Salmon and Steelhead in the Columbia River Basin. *North American Journal of Fisheries Management*, *8*(1), 1–24. https://doi.org/10.1577/1548-8675(1988)008<0001:EOHDAF>2.3.CO;2

Rechisky, E. L., Welch, D. W., Porter, A. D., Hess, J. E., & Narum, S. R. (2014). Testing for delayed mortality effects in the early marine life history of Columbia River yearling Chinook salmon. *Marine Ecology Progress Series*, *496*, 159–180. https://doi.org/10.3354/meps10692

Rechisky, E. L., Welch, D. W., Porter, A. D., Jacobs, M. C., & Ladouceur, A. (2009). Experimental measurement of hydrosystem-induced mortality in juvenile Snake River spring Chinook salmon using a large-scale acoustic array. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 1019–1024. https://doi.org/10.1139/F09-078

Rechisky, E. L., Welch, D. W., Porter, A. D., Jacobs-Scott, M. C., & Winchell, P. M. (2013). Influence of multiple dam passage on survival of juvenile Chinook salmon in the Columbia River estuary and coastal ocean. *Proceedings of the National Academy of Sciences*, *110*(17), 6883–6888. https://doi.org/10.1073/pnas.1219910110

Riddell, B. E., Brodeur, R. D., Bugaev, A. V., Moran, P., Murphy, J. M., Orsi, J. A., & Wertheimer, A. C. (2018). Chapter 5: Ocean Ecology of Chinook Salmon. In R. J. Beamish (Ed.), *The Ocean Ecology Of Pacific Salmon And Trout* (pp. 555–696). American Fisheries Society.

Roni, P. (2019). Does river restoration increase fish abundance and survival or concentrate fish? The effects of project scale, location, and fish life history. *Fisheries*, *44*(1), 7–19. https://doi.org/10.1002/fsh.10180

Ruff, C. P., Anderson, J. H., Kemp, I. M., Kendall, N. W., Mchugh, P. A., Velez-Espino, A., Greene, C. M., Trudel, M., Holt, C. A., Ryding, K. E., & Rawson, K. (2017). Salish Sea Chinook salmon exhibit weaker coherence in early marine survival trends than coastal populations. *Fisheries Oceanography*, *26*(6), 625–637. https://doi.org/10.1111/fog.12222

Ruggerone, G. T., & Irvine, J. R. (2018). Numbers and Biomass of Natural- and Hatchery-Origin Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean, 1925–2015. *Marine and Coastal Fisheries*, *10*(2), 152–168. https://doi.org/10.1002/mcf2.10023

Ryding, K. E., & Skalski, J. R. (1999). Multivariate regression relationships between ocean conditions and early marine survival of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences*, *56*, 2374–2384.

Sabal, M. C., Huff, D. D., Henderson, M. J., Fiechter, J., Harding, J. A., & Hayes, S. A. (2016). Contrasting patterns in growth and survival of Central Valley fall run Chinook salmon related to hatchery and ocean conditions. *Environmental Biology of Fishes*, *99*(12), 949–967. https://doi.org/10.1007/s10641-016-0536-3

Satterthwaite, W. H., Mohr, M. S., O'Farrell, M. R., Anderson, E. C., Banks, M. A., Bates, S. J., Bellinger, M. R., Borgerson, L. A., Crandall, E. D., Garza, J. C., Kormos, B. J., Lawson, P. W., & Palmer-Zwahlen, M. L. (2014). Use of genetic stock identification data for comparison of the ocean spatial distribution, size at age, and fishery exposure of an untagged stock and its indicator: California Coastal versus Klamath

River Chinook Salmon. *Transactions of the American Fisheries Society*, *143*(1), 117–133. https://doi.org/10.1080/00028487.2013.837096

Schaller, H. A., & Petrosky, C. E. (2007). Assessing hydrosystem influence on delayed mortality of snake river stream-type chinook salmon. *North American Journal of Fisheries Management*, *27*, 810–824. https://doi.org/10.1577/M06-083.1

Schaller, H. A., Petrosky, C. E., & Langness, O. P. (1999). Contrasting patterns of productivity and survival rates for stream-type chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*, 1031–1045.

Schindler, D., Krueger, C., Bisson, P., Bradford, M., Clark, B., Conitz, J., Winton, J. (2013). Arctic-Yukon-Kuskokwim Chinook Salmon Research Action Plan: Evidence of Decline of Chinook Salmon Populations and Recommendations for Future Research (pp. v + 70 pp.): Prepared for the AYK Sustainable Salmon Initiative (Anchorage, AK). v + 70 pp. Retrieved from http://www.aykssi.org/wp-content/uploads/AYK-SSI-Chinook-Salmon-Action-Plan-83013.pdf

Schoen, E. R., Wipfli, M. S., Trammell, E. J., Rinella, D. J., Floyd, A. L., Grunblatt, J., McCarthy, M. D., Meyer, B. E., Morton, J. M., Powell, J. E., Prakash, A., Reimer, M. N., Stuefer, S. L., Toniolo, H., Wells, B. M., & Witmer, F. D. W. (2017). Future of Pacific Salmon in the face of environmental change: Lessons from one of the world's remaining productive salmon regions. *Fisheries*, *42*(10), 538–553. https://doi.org/10.1080/03632415.2017.1374251

Seitz, A. C., Courtney, M. B., Evans, M. D., & Manishin, K. (2019). Pop-up satellite archival tags reveal evidence of intense predation on large immature Chinook salmon (*Oncorhynchus tshawytscha*) in the North Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(9), 1608–1615. https://doi.org/10.1139/cjfas-2018-0490

Sharma, R., & Quinn, T. P. (2012). Linkages between life history type and migration pathways in freshwater and marine environments for Chinook salmon, *Oncorhynchus tshawytscha*. *Acta Oecologica*, *41*, 1–13. https://doi.org/10.1016/j.actao.2012.03.002

Sharma, R., Vélez-Espino, L. A., Wertheimer, A. C., Mantua, N., & Francis, R. C. (2013). Relating spatial and temporal scales of climate and ocean variability to survival of Pacific Northwest Chinook salmon (*Oncorhynchus tshawytscha*). *Fisheries Oceanography*, *22*(1), 14–31. https://doi.org/10.1111/fog.12001

Skalski, J., Smith, S., Iwamoto, R., Williams, J., & Hoffmann, A. (1998). Use of passive integrated transponder tags to estimate survival of migrant juvenile salmonids in the Snake and Columbia rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 1484–1493. https://doi.org/10.1139/f97-323

Tomaro, L. M. (2010). *Year-class regulation of mid-upper Columbia River spring Chinook salmon* Oncorhynchus tshawytscha*: the role of juvenile size, growth, and migratory behavior.* (Master of Science). Oregon State University.

Tomaro, L. M., Teel, D. J., Peterson, W. T., & Miller, J. A. (2012). When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook salmon. *Marine Ecology Progress Series*, *452*, 237–252. https://doi.org/10.3354/meps09620

Tucker, S., Trudel, M., Welch, D. W., Candy, J. R., Morris, J. F. T., Thiess, M. E., Wallace, C., & Beacham, T. D. (2011). Life History and Seasonal Stock-Specific Ocean Migration of Juvenile Chinook Salmon. *Transactions of the American Fisheries Society*, *140*(4), 1101–1119. https://doi.org/10.1080/00028487.2011.607035

Waples, R. S., Teel, D. J., Myers, J. M., & Marshall, A. R. (2004). Life-history divergence in Chinook salmon: Historic contingency and parallel evolution. *Evolution*, *58*(2), 386–403. https://doi.org/10.1554/03-323

Weitkamp, L. A. (2009). Marine Distributions of Chinook Salmon from the West Coast of North America Determined by Coded Wire Tag Recoveries. *Transactions of the American Fisheries Society*, *139*(1), 147–170. https://doi.org/10.1577/T08-225.1

Weitkamp, L. A., & Neely, K. (2002). Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: Insight from marine coded-wire tag recoveries. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 1100–1115.

Welch, D. W., Boehlert, G. W., & Ward, B. R. (2002). POST–the Pacific Ocean Salmon Tracking Project. *Oceanologica Acta*, *25*(5), 243–253. https://doi.org/10.1016/S0399-1784(02)01206-9

Winton, J., & Hilborn, R. (1994). Lessons from supplementation of Chinook salmon in British Columbia. *North American Journal of Fisheries Management*, *14*(1), 1–13. https://doi.org/10.1577/1548-8675(1994)014<0001:LFSOCS>2.3.CO;2

Zabel, R. W., Faulkner, J., Smith, S. G., Anderson, J. J., Van Holmes, C., Beer, N., Iltis, S., Krinke, J., Fredricks, G., Bellerud, B., Sweet, J., & Giorgi, A. (2008). Comprehensive passage (COMPASS) model: A model of downstream migration and survival of juvenile salmonids through a hydropower system. *Hydrobiologia*, *609*(1), 289–300. https://doi.org/10.1007/s10750-008-9407-z

Zimmerman, M. S., Irvine, J. R., O'Neill, M., Anderson, J. H., Greene, C. M., Weinheimer, J., Trudel, M., & Rawson, K. (2015). Spatial and Temporal Patterns in Smolt Survival of Wild and Hatchery Coho Salmon in the Salish Sea. *Marine and Coastal Fisheries*, *7*(1), 116–134. https://doi.org/10.1080/19425120.2015.1012246

SUPPORTING INFORMATION

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

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