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Wild salmon and the shifting baseline syndrome: application of archival and contemporary redd counts to estimate historical Chinook salmon (*Oncorhynchus tshawytscha*) production potential in the central Idaho wilderness

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Abstract: The "shifting baseline syndrome" (SBS) is the paradigm whereby recent species abundances and environmental conditions are accepted as reflecting historical conditions. This leads to false impressions of the past, inaccurate baselines, and unrealistic recovery goals. Idaho biologists have counted Chinook salmon redds for >60 consecutive years, generating an invaluable database; however, inaccurate historical baselines compromise the utility of even such high-quality, long-term databases. To develop an accurate baseline, we integrated archival (1951–1964), maximum redd counts with contemporary (1995–2017), continuous counts and spawn timing datasets to estimate historical (1950s–1960s) wild Chinook salmon production potential. Current salmon populations average 3% of 1950s–1960s abundances, which may have been 30% of precommercial fishery (1880s) populations. Notably, the SBS has influenced contemporary managers as reflected in minimum viable abundance, sustainable escapement, and adequate seeding objectives equaling 10.4%, 17.9%, and 20.4%, respectively, of 1950s–1960s potential. Our approach provides a framework for utilizing archival and contemporary data to reconstruct historical baselines and repress SBS. Contrasting contemporary goals with maximum production potential provides new reference points and perspectives for managers to consider.

Résumé : Le « syndrome de la référence changeante » (SRC) est un paradigme selon lequel il est accepté que les abondances d'espèces et conditions ambiantes récentes reflètent les conditions passées. Il mène à des impressions erronées du passé, des états de référence inexacts et des objectifs de rétablissement irréalistes. Des biologistes en Idaho ont compté les nids de frai de saumons chinooks pendant plus de 60 années consécutives, produisant une base de données d'une valeur inestimable. Des états de référence passés inexacts compromettent toutefois l'utilité de bases de données de longue durée, même de cette qualité. Afin d'établir un état de référence exact, nous avons intégré les nombres maximums de nids de frai passés (1951–1964) aux résultats de dénombrements continus récents (1995–2017) et à des ensembles de données sur le moment du frai afin d'estimer le potentiel de production passé (années 1950 et 1960) de saumons chinooks sauvages. Les populations de saumons actuelles représentent en moyenne 3 % des abondances des années 1950 et 1960, qui représentaient possiblement 30 % des populations avant le début de la pêche commerciale (années 1880). Fait à noter, le SRC a influencé les gestionnaires actuels, comme en font foi les objectifs d'abondance viable minimum, d'échappement durable et d'ensemencement adéquat qui correspondent à 10,4 %, 17,9 % et 20,4 %, respectivement, du potentiel des années 1950 et 1960. Notre approche fournit un cadre d'utilisation des données d'archive et récentes pour reconstituer les états de référence passés et restreindre le SRC. La comparaison des objectifs actuels et du potentiel de production maximum fournit de nouveaux points de référence et de nouvelles perspectives que les gestionnaires devraient prendre en considération. [Traduit par la Rédaction]

Introduction

Long-term datasets represent a baseline against which one may examine current population status (Claro et al. 2009). Additional information is required, however, to accurately reflect historical potential. Pauly (1995) postulated that "the shifting baseline syndrome" (SBS) arises as each generation of scientists accepts as a baseline the stock size and species composition that occurred during their careers. As stocks further decline, the baseline shifts downward, accommodating the disappearance of species and inappropriate reference points for evaluating losses or identifying rehabilitation targets (Pauly 1995). Humphries and Winemiller (2009) observed that because overexploitation of fauna and disruption to ecosystems typically occurred decades before initial empirical stock assessments, often one can only imagine historic numbers. Consequently, managers may be deceived by SBS and incorrectly assume conditions of the immediate past reflect conditions in the intermediate and distant past (Humphries and Winemiller 2009). Such false impressions of past conditions impede our ability to set recovery targets and achieve them. Similarly, some diadromous species have declined steadily, fitting the SBS paradigm and resulting in establishment of inappropriate restoration goals (Limburg and Waldman 2009). For 35 time series, abundances of diadromous species dropped 98% and 90% of historic levels in 13 and 11 series, respectively (Limburg and Waldman 2009).

Since the 1940s, Columbia River basin (CRB) biologists have employed redd counts to monitor Chinook salmon (*Oncorhynchus*

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tshawytscha) population trends (Hassemer 1993; Emlen 1995). In Idaho, redd counts began in 1947 (Zimmer 1950; Schoning 1953) and counts with consistent methodologies have been maintained since the 1950s (Hassemer 1993). The resulting six-decade trend is of inestimable value (Isaak and Thurow 2006). Many biologists in the CRB are largely unaware of the magnitude of differences between former anadromous fish abundances and recent status (Lichatowich and Williams 2015) or of the production potential of systems with intact habitats.

The SBS is a fundamental obstacle to addressing global environmental issues (Soga and Gaston 2018) and compromises the utility of even the highest quality and longest termed fisheries databases if accurate estimates of historical production potential are unavailable. Inherent risks of SBS challenge biologists to more accurately estimate past abundances, distributions, and fish assemblages (Humphries and Winemiller 2009). Understanding the concept of shifting baselines helps neutralize denial (Jackson and Alexander 2011). A framework to maximize use of historical information and use of existing data to reconstruct historical conditions will help overcome SBS (Pauly 1995; Soga and Gaston 2018). In response to this need, we integrated archival, index-area redd counts with contemporary, spatially continuous redd counts and spawn timing databases to estimate historical (1950s–1960s) spring–summer Chinook salmon production potential in the Middle Fork Salmon River basin. We conclude with a discussion of salmon management and SBS, the importance of understanding historical biological potential and its value for informing recovery, factors that may affect contemporary production potential, and a framework for establishing sustainable management goals.

Materials and methods

Study area

The Middle Fork Salmon River (MFSR), one of eight original National Wild and Scenic Rivers designated in 1968 (National Wild and Scenic River System (NWSRS), https://www.rivers.gov/rivers/salmon-mf-id.php, accessed October 2018), drains about 7330 km^2 of a remote area of central Idaho and, for most of its length, flows through the Frank Church River of No Return Wilderness (FC-RONRW). From its origin at the confluence of Bear Valley and Marsh creeks, the MFSR flows north–northwest for 171 km through the Salmon River Mountains and joins the Salmon River 92 km downstream from Salmon, Idaho (Fig. 1), and 1144 km from the Pacific Ocean. Minshall et al. (1981), Thurow (2000), and Servheen et al. (2001) provide more detailed study area descriptions. Native fishes are represented by five families (Catostomidae, Cottidae, Cyprinidae, Petromyzontidae, and Salmonidae), 10 genera, and 16 species (Thurow 1985). Seven salmonid taxa include anadromous summer steelhead (*Oncorhynchus mykiss*) and spring–summer Chinook salmon. Only brook trout (*Salvelinus fontinalis*) are nonindigenous (see online Supplementary material[1]).

Within the MFSR, spring-run Chinook salmon (Matthews and Waples 1991) predominate, although summer-run fish occur sympatrically with spring-run fish in several drainages. Our observations of MFSR fish are consistent with those reported by Matthews and Waples (1991); spring-run fish spawn earliest in higher elevation headwater stream reaches compared with summer-run fish that spawn later at lower elevations.

As Euro-Americans settled the northwestern USA, the distribution and abundance of Chinook salmon declined (Nehlsen et al. 1991; National Research Council (NRC) 1996; Lee et al. 1997). Concern for the persistence of Snake River Chinook salmon culminated in a final rule (Office of the Federal Register 57 [April 22, 1992]:23458) that listed Snake River spring–summer Chinook salmon as "Threatened" under the Endangered Species Act of 1973 (ESA). Federal fisheries management agencies summarized the "four H's" (habitat degradation, harvest, hatchery practices, and hydrosystem operation) as primary causes of CRB anadromous fish declines (National Marine Fisheries Service (NMFS) 2000).

Our study area is unique within the CRB because not all four "H's" apply to its salmon populations. First, Chinook salmon stocks in the MFSR basin are wild, indigenous, and unaltered by direct hatchery supplementation. The MFSR is managed as a designated wild anadromous fish sanctuary with the objective of preserving the genetic integrity of wild, native salmonids (Idaho Department of Fish and Game (IDFG) 2019). Consequently, the production potential of the basin and the ability of salmon to respond to the quality and quantity of available natal habitat have not been altered. Wild, indigenous, Chinook salmon populations such as those in the MFSR are rare; Thurow et al. (2000) reported their presence in 4% of the potential historical range and 15% of the current range in the interior CRB and portions of the Klamath River basin. Second, natural processes in the MFSR function relatively unimpeded by humans. Natal habitats remain diverse, high quality, and connected (Thurow 2000, 2015; Isaak and Thurow 2006). Within most of the drainage, habitat quality has not been substantially altered by anthropogenic activities, and exotic fishes are uncommon. Minimal anthropogenic effects and a geographic size that facilitates the existence of natural processes including wildfire, floods, debris flows, and snow avalanches ensure continual generation and maintenance of a diversity of stream habitats (Isaak et al. 2003; Thurow 2015). About 800 km of tributaries and the mainstem are accessible to Chinook salmon (Mallet 1974; Thurow 1985), and connectivity among its populations is high (Fullerton et al. 2016). Third, harvest rates are low. Ocean harvest rates based on coded wire tags were <1% (Schaller et al. 2014). The treaty and non-treaty harvest of wild Snake River spring Chinook salmon in the Columbia River averaged 9.2% from 1980 to 2018 (Joint Staff Report 2019). Idaho sport anglers must release all wild fish and the Tribal harvest is low. For example, in 2017, the Nez Perce Tribe harvested no fish in Big Creek or at Dagger Falls and the Shoshone–Bannock Tribes harvested 10 fish in Bear Valley and Marsh creeks (J. Oatman, Nez Perce Tribe, Lapwai, ID 83540, USA, and K. Tardy, Shoshone–Bannock Tribes, Fort Hall, ID 83203, USA, respectively, personal communications).

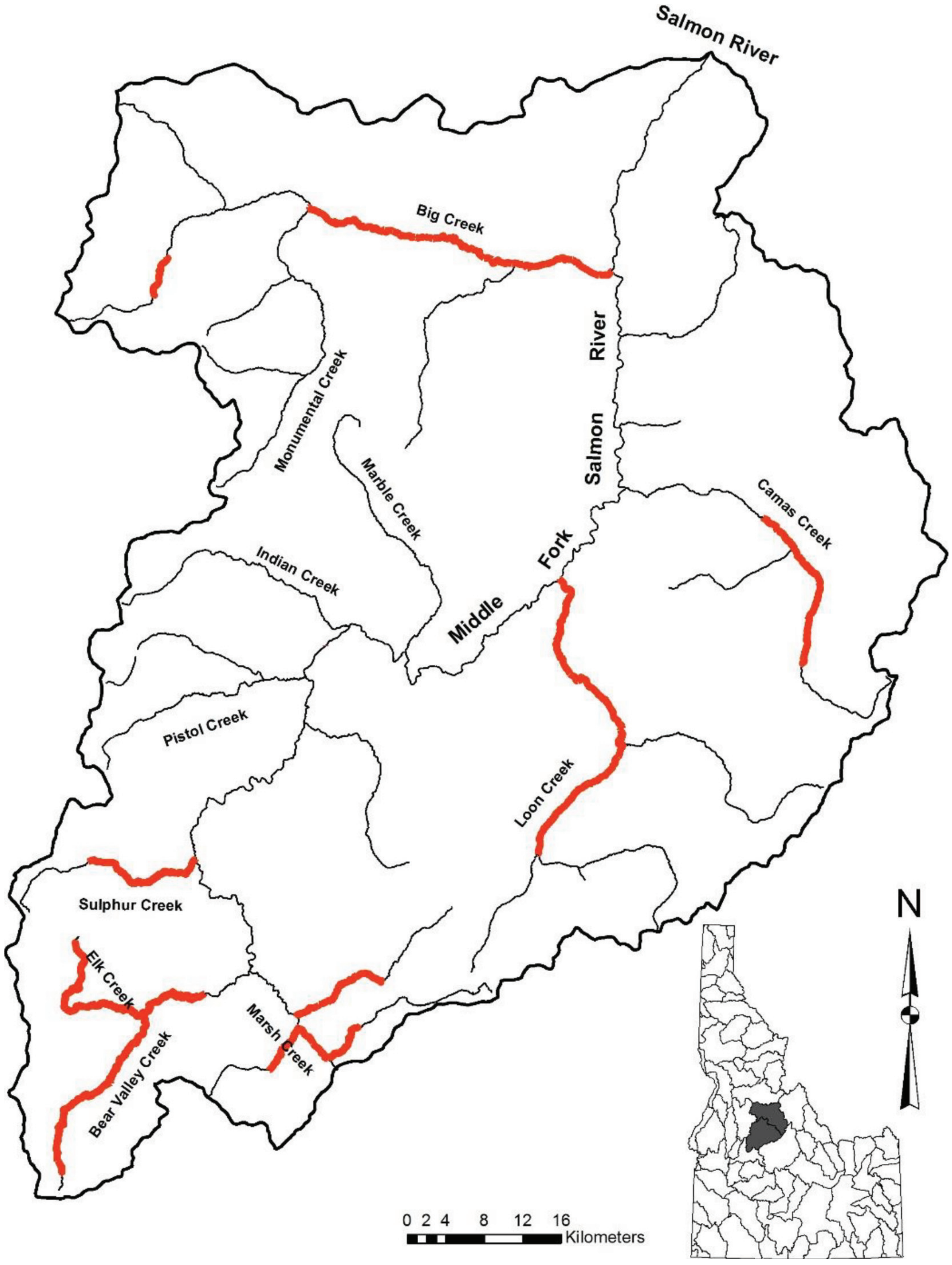
Despite abundant, high-quality natal (spawning and rearing) habitat, absence of hatchery fish, and low harvest rates, MFSR Chinook salmon and steelhead remain at risk of extirpation, primarily as a result of factors outside the MFSR basin within the migration corridors of the Columbia and Snake rivers, estuaries, and the ocean. Habitat conditions throughout most of the MFSR are in excellent condition, and key limiting factors affecting these populations are from outside natal spawning and rearing areas (NMFS 2017).

Archival IDFG redd counts

In our analysis, we integrated archival redd counts with contemporary redd census and spawn timing datasets to estimate historical (1950s–1960s) Chinook salmon production potential. We utilized archival, index-area redd count data collected from 1951 to 1964 (Table 1). In 1951, the IDFG began surveying Chinook salmon redds within the MFSR. From 1951 to 1953, redds were surveyed using fixed-wing aircraft (Hauck 1953, 1954). Aerial counts were compared with ground-based counts in certain stream reaches, and the author noted that aerial counts were less accurate (i.e., more errors of omission) in smaller streams (i.e., Camas Creek) compared with mainstem rivers. Aerial counts also had more omissions in stream reaches with shadows resulting from canopy or topography. From 1953 to 1956, the IDFG surveyed major MFSR tributaries, defined as those with a minimum spawn-

[1]Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0111.

Fig. 1. Middle Fork Salmon River drainage, Idaho, and location of index reaches (highlighted) in six major tributaries.



ing escapement of 200 adult salmon; surveys included both aerial (fixed-wing aircraft) and ground-based redd counts (Richards and Gebhards 1959) (see online Supplementary material[1]).

In 1957, the IDFG began annually counting Chinook salmon redds in six major MFSR tributaries (Fig. 1), establishing "index reaches" that supported major concentrations of spawning Chinook salmon. Index reaches were consistently counted during "peak" spawning periods, when it was assumed that a majority of redds would be observed (Schwartzberg and Roger 1986) and an accurate measure of the population trend (e.g., Hassemer 1993) would be obtained. Hassemer (1993) summarized and reviewed the Idaho redd count data from 1957 to 1992.

More recently, Elms-Cockrum (2001) summarized the index-area redd count methodology as follows: "Single peak-count surveys are made over each trend area each year. The surveys are timed to coincide with the period of maximum spawning activity on a particular stream, and each transect is therefore assigned a target count-time window based on historic observations. Redd counts are made depending on the best visual technique for a particular trend area. The consistency and accuracy of redd counts can be maintained over time by following these standard procedures, and variability or bias caused by observer changes and hydrologic events can be minimized." Annual, index-area redd counts continue today within the same six MFSR tributaries and

Table 1. Maximum Chinook salmon redd counts in archival and non-archival stream reaches in the mainstem Middle Fork Salmon River (MSFR) and tributaries, 1951–1964, including survey dates, methods, data sources, and unsurveyed distances.

Drainage	Stream	Reach description or IDFG number (Hassemer 1993)	Maximum redd count	Count date	Method	Data source	Unsurveyed distance (km)
Bear Valley Creek	Bear Valley	WS-9a,b,c,d + WS-10a,b	791	2 September 1957	Fixed wing + ground count	Metsker 1958	6.86
	Elk	WS-11b,c	266	3 September 1963	Fixed wing + ground count	Hassemer 1993	4.48
	Elk	WS-11a	388	24 August 1963	Fixed wing + ground count	Hassemer 1993	0.00
	Minor Bear Valley tributaries	Cache, Fir, Pole, Sack, Sheep, Trail Creeks	44	23 September 1952	Ground count	Hauck 1952*a*	Unknown
	Elk Creek tributary	Bearskin Creek	14	3 September 1958	Ground count	Richards and Gebhards 1959	2.05
Big Creek	Big	WS-13	377	30 August 1961	Ground count	Hassemer 1993	20.80
	Big	WS-14c, 14d	465	2 September 1957	Fixed wing	Hassemer 1993	1.08
Camas Creek	Camas	WS-8	177	4 September 1964	Fixed wing	Hassemer 1993	17.48
	Camas	Castle Creek to South Fork Camas Creek	102	15 August 1964	Fixed wing	Hassemer 1993	8.81
Loon Creek	Loon	WS-6 + WS-7	425	4 September 1957	Fixed wing + ground count	Hassemer 1993	48.40
Marsh Creek	Marsh	WS-2a,b	332	26 August 1964	Ground count	Hassemer 1993	10.70
	Capehorn	WS-3	138	20 August 1964	Ground count	Hassemer 1993	0.22
	Knapp	WS-4	57	14 August 1964	Ground count	Hassemer 1993	7.07
	Beaver	WS-5	182	22 August 1964	Ground count	Hassemer 1993	6.52
Pistol Creek	Pistol	Confluence to Popgun Creek	38	10 September 1955	Fixed wing	Pirtle 1956	26.44
Sulphur Creek	Sulphur	WS-12 + OS-4	544	27 August 1954	Fixed wing + ground count	Pirtle 1956	4.97
Mainstem MFSR	Entire length	WS-15 + upstream	425	15–17 September 1951	Fixed wing	Hauck 1952*a*	0.00

the mainstem MFSR with assistance from tribal and federal collaborators (Hassemer 1993; Stiefel et al. 2016).

Contemporary redd census

Since 1995, USDA Forest Service, Rocky Mountain Research Station (RMRS) biologists have expanded the above-referenced IDFG archival redd counts with spatially continuous redd surveys encompassing all potential Chinook salmon spawning areas within the MFSR (Thurow 2000). RMRS goals were to improve monitoring of ESA-listed MFSR Chinook salmon populations and to improve understanding of the spatial and temporal characteristics of salmon population dynamics. The spatially continuous surveys were also developed to complement index-area surveys, provide more accurate escapement estimates, and increase analytical power (Isaak and Thurow 2006). Although index-area counts can provide population trends, index areas have limitations because they may not represent the dynamics of salmonid populations at larger scales (Rieman and McIntyre 1996). Index-area counts may also omit redds as a result of annual variation in spatial distributions or spawning activity (Maxell 1999; Dunham et al. 2001). Lack of randomization in site selection and shifts in fish distribution may also bias index-area monitoring and mask population trends (Isaak and Thurow 2006). Spatially continuous census techniques overcome many of the limitations associated with traditional sampling designs (Isaak and Thurow 2006), including index-area surveys. RMRS annually surveyed all potential Chinook salmon spawning areas at the end of the spawning period and confined its surveys to non-index streams and index areas where multiple pass surveys were not being completed. This approach efficiently avoided re-surveying areas where experienced state, tribal, and U.S. Forest Service biologists collected total redd abundance data and georeferenced individual redds (see online Supplementary material[1]).

Potential spawning areas were identified in 12 tributaries and the mainstem MFSR by reviewing past redd locations and juvenile Chinook salmon occurrence, inspecting anecdotal redd accounts, and contacting biologists familiar with the drainage (Thurow 2000). Surveyed stream reaches totaled nearly 700 km of potential, accessible spawning habitats (Fig. 1).

Spatially continuous surveys were conducted annually after Chinook salmon had completed spawning and while redds remained visible, in contrast to IDFG index-area surveys at "peak" spawning times. MFSR Chinook salmon spawn timing varies among sites and typically begins in late July in the highest elevations (1800–2100 m) and continues until the second week in September in the lowest elevations (1000–1300 m) (R. Thurow, unpublished data). Consequently, redd surveys typically began at the highest elevations in early September and were completed in lower elevations from 11 to 14 September. Salmon spawned later during larger escapements. To achieve a complete census, from 2001 to 2003 (>1500 redds), RMRS completed a second, late-September survey of the lower mainstem MFSR and lower Big Creek.

Low-level helicopter flights provided annual, spatially continuous Chinook salmon redd surveys within that portion of the stream network described previously (Fig. 1). Aerial surveys between 0900 and 1800 h enhanced direct overhead light and improved visibility. To avoid introducing interobserver bias (Dunham et al. 2001), all RMRS aerial surveys and ground-based surveys were conducted by the same observers (R. Thurow (RMRS) and J. Guzevich (RMRS), respectively). An experienced backcountry pilot flew a turbine helicopter and maintained very slow airspeeds (10–15 knots) at low altitudes (15–50 m) above the stream bed, depending on the surrounding terrain. The helicopter also facilitated re-flying challenging areas. When redds were observed, a global positioning system (GPS; Pathfinder ProXL, Trimble, Sunnyvale, California) georeferenced and recorded locations. All GPS locations were differentially corrected with known base stations. RMRS assembled data into a geographic information system (GIS) and developed annual, cumulative GIS maps and databases of individual redds.

Redd dimensions are proportional to female length (Crisp and Carling 1989), and MFSR Chinook salmon were similar to those measured by King and Thurow (2000). Dense riparian canopy precluded aerial observation in some reaches and the experienced ground-based observer annually walked those streams and recorded redd coordinates with a handheld GPS. Both aerial and ground-based observers wore polarized sunglasses and searched potential spawning areas for the characteristic pit and tailspill morphology of Chinook salmon redds (Burner 1951). Discerning salmon redds from those of other fall-spawning salmonids (e.g., bull trout, *Salvelinus confluentus*) was not problematic, given the larger size of salmon redds and earlier time of construction. Redd count validation based on intensive, replicated ground surveys suggested a strong relationship between aerial counts and "true" counts (Thurow and McGrath 2010). Because we were unable to quantify other sources of error in the RMRS database, we assumed that annual redd counts were without error, the classical design-based approach to statistical inference (Thompson 1992; Courbois et al. 2008).

Timing of redd construction

We empirically measured redd construction dates and merged data from two sources: RMRS multiple-pass ground-based redd surveys and the IDFG Idaho Supplementation Study (Venditti et al. 2015). RMRS surveys recorded spawn timing data in five of seven major tributaries (excluding Marsh and Pistol creeks), and IDFG biologists collected timing data in Marsh Creek (Table 1). From 2001 to 2005, RMRS biologists completed intensive ground-based redd surveys that began prior to redd construction and continued at 4–5 day intervals until all redds were completed. IDFG completed an average of three multiple-pass redd surveys in sections of Marsh Creek and its tributaries Beaver, Cape Horn, and Knapp creeks during the same years (Bruce Barnett (IDFG), personal communication). Together, these data documented differences in the timing of redd construction across drainages and between lower and upper elevation reaches within the same streams.

Analytical approach for estimating historical production potential

We applied a multistep approach for estimating historical redd production potential using the three previously described (archival index-area, contemporary census, and redd timing) datasets. Archival redd counts completed by the IDFG in the 1950s–1960s provided the foundation for our MFSR production estimates; however, these single-pass archival surveys frequently did not encompass all available suitable spawning habitat or count redds after peak spawning. Therefore, to estimate production potential, we sought to include redds constructed within index reaches after peak spawning (temporal expansion) and redds constructed in stream reaches that the IDFG did not survey (spatial expansion). We applied contemporary data that described temporal and spatial characteristics of redds to adjust archival IDFG counts and more accurately estimate potential redd abundances. We created vectors of the potential expansion values at each step and sampled from the value distributions (with replacement) at subsequent steps (Fig. 2). This approach captured the essential variability in the data (except for the maximum redd count, which was treated as fixed).

Archival maximum counts

We inspected archival, index-area redd counts conducted by the IDFG in the 1950s and 1960s to identify maximum redd counts in the MFSR. We selected these data because they include the largest recorded redd counts prior to severe salmon population declines that began in the late 1960s. Chinook salmon smolt survival in the Snake River significantly declined after completion of the Lower Monumental Dam in 1969 and the Little Goose Dam in 1970 (Raymond 1979).

We located archival redd surveys with maximum redd counts in six major MFSR spawning tributaries plus the mainstem MFSR (Table 1). As described above, most IDFG index-area surveys were conducted during "peak" spawning prior to the end of spawning. As a result, the archival surveys did not count redds constructed after the peak spawning date. Individual reaches in larger drainages were often surveyed separately, and dates of maximum counts varied, e.g., in two Big Creek reaches. The maximum count in the mainstem MFSR was recorded during an aerial survey of six consecutive reaches within 3 days in 1951. We also found maximum counts in several smaller tributaries to Bear Valley Creek that were not repeated until contemporary times (Bearskin, Cache, Fir, Pole, Sack, and Sheep Trail creeks). For the four remaining known spawning tributaries (Indian, Marble, and Pistol creeks and Rapid River), only Pistol Creek had records of a reliable maximum redd count. Surveys of the other drainages did not span a significant proportion of their suitable spawning habitat and were unsuitable for estimating maximum potential. Consequently, we applied another approach, described in the next section, to estimate historical production in the three minimally surveyed streams.

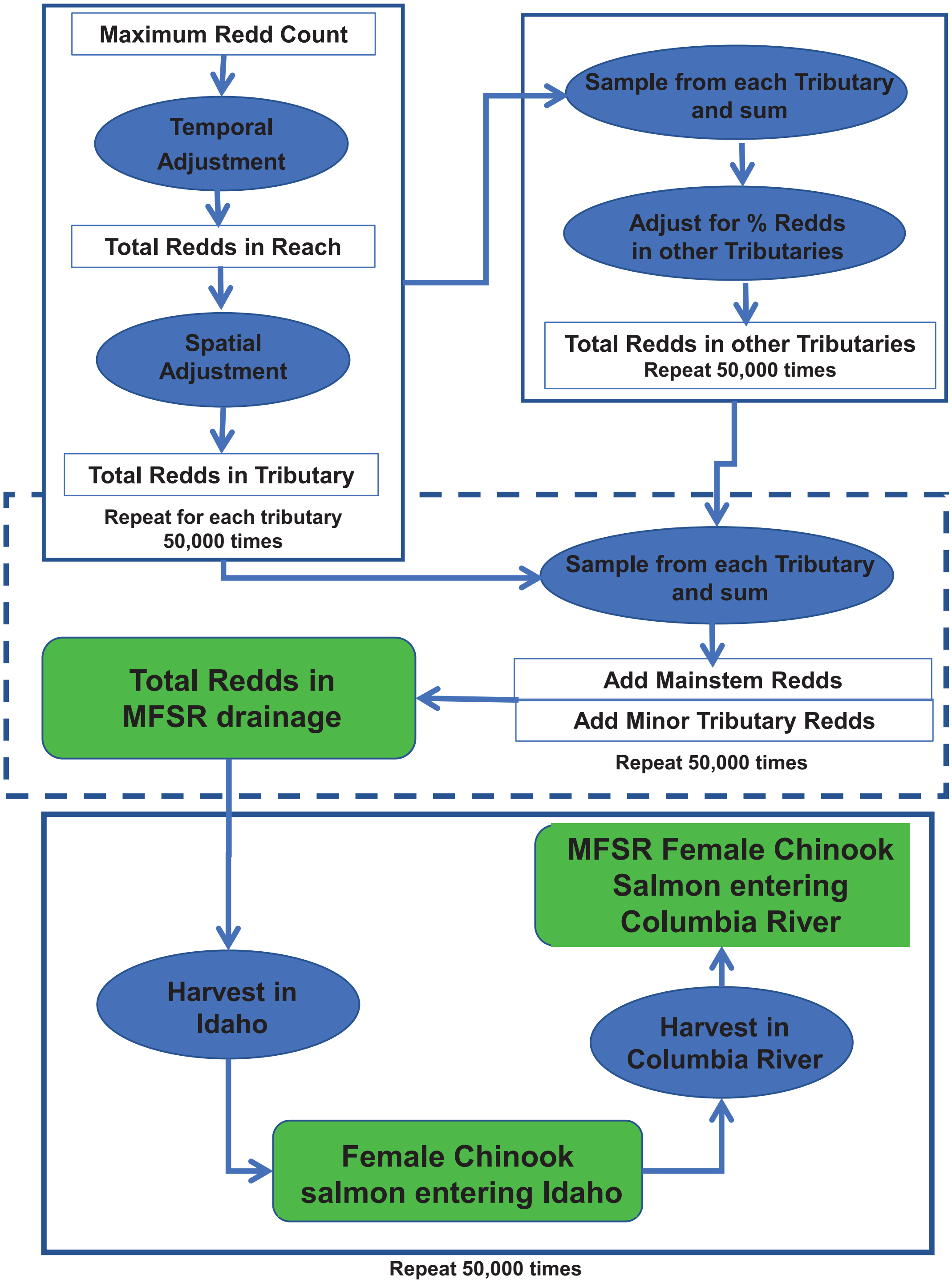
Temporal adjustment of maximum counts

Most archival, maximum counts were completed during a "peak" spawning period that did not account for all redds. As a result, we applied a temporal adjustment to remove temporal bias and estimate total redds constructed. Maximum redd counts were adjusted using contemporary, empirical information to describe the timing of MFSR salmon redd construction. We applied the contemporary redd construction timing data to estimate the percentage of redds constructed by the date of the archival, maximum redd count. We matched spawn timing data with the boundaries of stream sections with maximum redd counts. Big Creek maximum redd counts were separated into two sections each, and we applied discrete timing adjustments to each section. We applied contemporary timing data to temporally adjust archival, maximum redd counts in six major drainages and 12 stream sections. Available years of timing data ranged from three to five, with a median of four (see online Supplementary material, Table S1 and Fig. S1[1]).

To estimate the percentage of total redds completed each year by date, we plotted the 2001–2005 data annually by stream reach as a cumulative distribution curve. The percentage of total redds completed by the date of the maximum redd count was either read directly from the graph or interpolated between two points on the graph (see online Supplementary material, Fig. S1[1]). For example, the maximum redd count in lower Loon Creek was recorded on 4 September 1957. Redd timing data collected in lower Loon Creek in 2001 indicated that 79% of redds (read directly from the plot) were constructed by 4 September.

Counts in several tributary reaches did not require temporal adjustments because they were completed late enough to provide an accurate estimate of the total number of redds constructed throughout the spawning period. For example, maximum redd counts in Pistol Creek were completed on 10 September 1955 (Table 1). Data from Sulphur and Loon creeks, streams with timing

Fig. 2. Flow chart illustrating the analytical approach used to estimate the total number of redds that would have been observed in the Middle Fork Salmon River drainage in the 1950s–1960s if all potential spawning areas had been surveyed after all redds were constructed, and the analytical approach used to estimate the total number of female Chinook salmon destined for the Middle Fork Salmon River drainage in the 1950s–1960s provided no freshwater harvest had occurred in Idaho or the Snake or Columbia rivers.



data geographically closest to those in Pistol Creek, coupled with observations during RMRS continuous surveys over the past 23 years, confirmed that most redds in Pistol Creek were constructed by 10 September.

The mainstem MFSR was aerially surveyed from 15 to 17 September 1951 (Table 1). Hauck (1951) reported that the 1951 escapement of adult Chinook salmon into the Salmon River basin was "good to excellent" compared with runs in prior years. In 2003, adult salmon escapements were the largest since the 1980s and five of 33 mainstem redds (15.2%) were constructed nearly 10 days later than the maximum count date (24–26 September versus 15–17 September). As a result, it is very likely that late-spawning Chinook salmon constructed additional redds after 17 September 1951. However, because we had only 2003 data to estimate the proportion of later redds, we did not temporally adjust the 1951 maximum count.

Spatial adjustment of maximum counts

Most archival redd counts were also spatially biased by the exclusion of spawning reaches outside surveyed index areas. To account for this bias, we applied contemporary, continuous redd counts to spatially adjust maximum redd counts in two stages. First, we estimated the total number of redds in each stream with archival, maximum redd counts. Next, we applied contemporary redd counts to estimate the percentage of total redds constructed within the same reaches surveyed during archival, maximum redd counts. For example, the Loon Creek drainage supported redds in reaches surveyed during the archival, maximum survey, as well as in non-surveyed reaches of Loon Creek and its tributaries, Warm Springs and Mayfield creeks. Thus, we expanded the maximum Loon Creek count to encompass the reaches that were not surveyed during the archival, maximum count (see online Supplementary material, Table S2 and Fig. S2[1]).

We applied the results of 1995–2017 RMRS continuous redd counts to develop spatial adjustments of the maximum counts. Isaak and Thurow (2006) reported that at very low adult escapements, the distribution of spawning Chinook salmon in the MFSR contracted into a small number of "core areas". Consequently, at low escapements, the distribution of redds no longer reflected the available habitat. We inspected redd distributions across the 23 years of continuous data and observed that when fewer than 250 redds were observed, many stream reaches supported zero or very few redds. For example, in 1995, only five of 10 major drainages supported redds. Consequently, we excluded years 1995, 1996, 1999, and 2017. Hence, we applied 19 years of data to estimate the percentage of total redds constructed within the same reaches surveyed during the archival, maximum redd counts.

We divided the archival, maximum redd count by the percentage of redds constructed in that reach during continuous redd surveys to estimate the total redds constructed in the entire tributary. In streams with archival, maximum counts in multiple sections (Big, Camas, and Marsh creeks), we summed the data and performed one spatial adjustment. The percentage of redds used in the spatial adjustments varied by stream and year. In Sulphur Creek, most available spawning areas were surveyed; from 95.9% to 100% of redds were observed in the archival surveyed reach, and redds were seen outside that reach in two of 19 years. Conversely, in Pistol Creek, many redds (median of 38.5%) were observed outside the archival, index-area reach, and some redds lay outside the index-area reach all 19 years.

In the second stage, we estimated the total redds constructed in all remaining spawning areas within the MFSR drainage in the 1950s–1960s. In three remaining tributaries with no reliable maximum archival counts (Indian and Marble creeks and Rapid River), we applied the 1995–2017 RMRS continuous redd count data (excluding the 4 years noted earlier) to estimate the percentage of all tributary redds observed in these three minimally surveyed tributaries. During the 19 years of data from 1995 to 2017, the median proportion of redds observed in these three streams averaged 4.1% and varied from 2.0% to 9.6%.

Harvest adjustment of total redds

Our goal was to estimate the maximum potential number of redds in the MFSR basin, so we adjusted estimated total redds by sport, commercial, and tribal harvest rates in the 1950s–1960s to estimate the number of redds that would have been constructed if the entire salmon return had been unharvested and allowed to reach MFSR spawning areas, assuming negligible natural mortality (Fig. 2). First, we obtained estimates of sport, commercial, and tribal harvest rates on adult spring–summer Chinook salmon during the 1950s–1960s in the Columbia, Snake, Salmon, and Middle Fork Salmon rivers. We selected archival, maximum redd counts from a 14-year period (1951–1964). We applied harvest rates from this identical time period and calculated conversion rates through the sport, tribal, and commercial fisheries in the CRB to estimate numbers of Chinook salmon that entered the Columbia River and were destined for the MFSR. Schaller et al. (2014) computed conversion rates for MFSR populations and we used their estimates for 1957–1964. These authors also computed mainstem harvest rates (Columbia River estuary to Snake River) dating back to 1951, compiled by the joint staffs of the Oregon Department of Fish and Wildlife and the Washington Department of Fish and Wildlife, and the U.S. versus Oregon Technical Advisory Committee (C. Petrosky (IDFG, Boise, ID 83707, USA), personal communication). We used the mainstem rates and then applied 1951–1956 Idaho sport harvest information reported by Hauck (1952*a*, 1952*b*, 1954), IDFG (1954, 1955), and Pirtle (1958) to extend the MFSR conversion rate estimates back to 1951 (see online Supplementary material, Table S3[1]).

Where possible, we used reported harvest rates specific to the MFSR. In other cases, we divided estimated harvest by reconstructed salmon abundance (from the above-referenced reports) to derive a harvest rate. We also included a nominal 5% tribal harvest rate, consistent with Schaller et al. (2014).

We multiplied all conversion rates together (1 – harvest rate) and divided the MFSR total redd estimate by the product. Estimated total harvest rates were substantial from 1951 to 1964. The median total harvest rate was 60% and ranged from 49% in 1958 to 76% in 1956. The median conversion rate from the Columbia River estuary to MFSR spawning grounds was 40% and ranged from 24.1% to 51.4%. We used a bootstrap procedure to perform harvest rate adjustments and estimate the potential number of female Chinook salmon that would have returned to the MFSR without harvest (Fig. 2).

Bootstrap and summation

Considerable uncertainty attended the extrapolation of archival and contemporary data necessary to achieve our goals. Therefore, we used bootstrap procedures at each temporal and spatial expansion to derive point estimates based on a distribution of reasonable values. We report the median, mean, maxima, minima, and quartiles. In three steps, we generated a distribution of the potential maximum number of redds in the MFSR in the 1950s–1960s (Fig. 2). In each bootstrapping step, we sampled from the potential values with replacement 50 000 times.

In step 1, we sampled from the temporal expansions for the stream reaches for which this step was necessary. The 2001–2005 data provided a range of redd completion dates across several years, so we used a bootstrap procedure to perform temporal adjustments and estimate the total number of redds that would have been observed if the archival redd counts had been completed after all redds were constructed (Fig. 2). Spatially continuous redd distribution data provided a range of values across 19 years, and we similarly applied a bootstrap procedure to perform spatial adjustments and estimate redds. The spatial procedure provided an estimate of the total number of redds that would have been observed if the archival redd counts had surveyed all available spawning areas across all drainages (Fig. 2). We bootstrapped data from each reach independently, divided them by the percentage of redds sampled from the spatial expansion factors for individual streams, and saved all 50 000 values by stream.

In step 2, the estimated number of redds in minimally surveyed Indian and Marble creeks and Rapid River were computed as a group. We generated a distribution of redds in the remainder of the MFSR by sampling from each of the other streams, adding them, and then dividing by an expansion factor sampled from the three minimally surveyed tributary expansion factors. These values were saved such that there were 12 stream-specific datasets to draw from for the final step. In the final step, we sampled from each dataset, summed the 12 values, added redds from unexpanded reaches, and saved to generate the distribution of the potential number of redds in the MFSR.

We used archival harvest rates to generate a distribution of the number of redds that would have been constructed if the entire Chinook salmon run destined for the MFSR had been unharvested and allowed to reach spawning areas (Fig. 2). Biologists have consistently reported the construction of one redd per female for spring–summer Chinook salmon (Gallagher and Gallagher 2005; Murdoch et al. 2009), so we assumed that the number of female Chinook salmon that returned to the MFSR was equivalent to the potential number of redds constructed. We sampled from the total redd distributions and divided them by a value sampled from the conversion factor values from 1951–1964. We multiplied together all sources of harvest mortality and divided the total MFSR redd estimate by the percent unharvested (1 – total harvest rate). The potential number of females equaled the potential number of redds. We saved results and generated a distribution of the maximum potential number of redds in the MFSR. Finally, we compared our estimate of historical (1950s–1960s) maximum redd production potential with contemporary Chinook salmon abundances estimated from the RMRS redd census since 1995.

Results

We documented maximum redd counts reported from 1951 to 1964 in the mainstem MFSR and in 10 tributary spawning reaches distributed within Bear Valley and Elk creeks (two reaches); Big Creek (one reach); Camas Creek (one reach); Loon Creek (one reach); Marsh, Beaver, Capehorn, and Knapp creeks (four reaches), and Sulphur Creek (one reach) (Table 1). Most maximum tributary counts were reported from 1957 to 1964. Exceptions were in Sulphur Creek in 1954, five tributaries to Bear Valley Creek in 1952 (Hauck 1952*a*), the Pistol Creek drainage in 1955 (Pirtle 1956), and in one Elk Creek tributary in 1958 (Table 1) (Richards and Gebhards 1959). The maximum mainstem MFSR redd count was reported in 1951 (Table 1).

Maximum redd counts were observed on dates ranging from 14 August 1964 in Knapp Creek to 23 September 1952 in Bear Valley Creek tributaries (Table 1). Most maximum counts were observed in late August and early September. The proportion of redds observed by the maximum count dates varied widely across streams and years.

The proportion of potential spawning areas surveyed during archival redd counts also varied widely. All potential spawning areas in the mainstem MFSR were surveyed in 1951, so no spatial expansion was necessary (Table 1). In contrast, each tributary spawning area contained unsurveyed stream reaches, so those counts required spatial expansions. Unsurveyed reaches requiring spatial expansions ranged from relatively short distances (e.g., 6.86 km of Bear Valley Creek and 4.48 km of Sulphur Creek) to much longer unsurveyed stream reaches (e.g., 48.4 km of Loon Creek) (Table 1). The drainages of Big, Camas, Marsh, and Pistol creeks each had more than 20 km of unsurveyed spawning reaches (Table 1).

Historical (1950s–1960s) Chinook salmon production potential

We estimated that 6279 to 12 938 redds were annually constructed in the MFSR basin in the 1950s–1960s (Fig. 3). The median and mean equaled 8783 and 8815 redds, respectively, with an interquartile range from 8192 to 9411 redds. These values represent our best estimate of the potential number of redds that would have been observed in the mainstem MFSR and tributaries (after downstream harvest) if all spawning areas had been completely surveyed after all redds were constructed and remained visible.

The potential number of female Chinook salmon that entered the Columbia River and were destined for the MFSR ranged from 12 691 to 49 995 in the 1950s–1960s (Fig. 3). The median and mean equaled 23 022 and 24 304 females, respectively, with an interquartile range of 19 953 to 28 047. It is noteworthy that the distribution is skewed to more values larger than the median and mean than values less. Hence, the MFSR basin potentially supported an estimated 24 000 redds constructed by 24 000 female Chinook salmon in the 1950s–1960s, prior to severe population declines that began in the late 1960s.

Discussion

MFSR production potential and relevance for establishing management goals

Chinook salmon production was historically high in the MFSR, and the maximum production potential remains high. The MFSR retains important building blocks for recovery: (*i*) abundant, diverse, and high-quality connected habitat; (*ii*) genetic diversity and no evidence of genetic bottlenecks; (*iii*) high life history diversity; and (*iv*) resiliency (NMFS 2017, chapter 5). Although conditions are degraded in small, localized areas outside wilderness, habitats throughout most of the MFSR are in excellent condition (NMFS 2017). Historical grazing, mining, and road impacts are being mitigated by natal habitat restoration efforts outside wilderness boundaries in Bear Valley, Big, Marsh, Loon, and Sulphur creeks (NMFS 2017). Within Bear Valley Creek, for example, the Shoshone–Bannock Tribes completed rehabilitation of upper valley dredge mining areas, and by 2001, all grazing allotments adjacent to Bear Valley and Elk creeks had been purchased and retired (NMFS 2017).

Consequently, our estimate of approximately 24 000 female or 48 000 total adult Chinook salmon destined for the MFSR provides a more accurate baseline for establishing production potential and informing management goals. Several current management goals do not address production potential. NMFS' recent "viability goal" of 2500 redds is about 10.4% of our estimated potential (NMFS 2017); however, by definition, this viability goal equals the "minimum" number of adult salmon needed to avoid a high risk of extirpation. The Nez Perce Tribe's "sustainable escapement objective" (which includes terminal harvest) equals 4300 redds (NPT 2013) or about 17.9% of our estimated potential; and the IDFG's "adequate seeding goal" of 4890 redds (IDFG 1992) is about 20.4%. Although these latter two goals strive to produce a desired level of harvest on a sustainable basis, they neither include maximum sustainable harvest objectives nor strive for maximum production potential.

Other, recent management goals do acknowledge much larger production potential in the MFSR. In their updated Fisheries Management Plan, IDFG described a "healthy and harvestable" goal that extends beyond minimum abundance thresholds adopted in ESA recovery plans (IDFG 2019). Because the MFSR drainage supports about 87% of the total MPG population, the "healthy and harvestable" IDFG goal for the MFSR equals 19 130 wild fish (9565 redds). The Nez Perce Tribe's "ecological escapement objective" of 43 000 redds (NPT 2013) also acknowledges larger production potential. This latter goal strives for maximum production that would sustain high harvest levels and ecological services. Because 43 000 redds exceeds our 1950s–1960s salmon production potential estimate of 24 000 redds, managers may question if this higher objective is achievable.

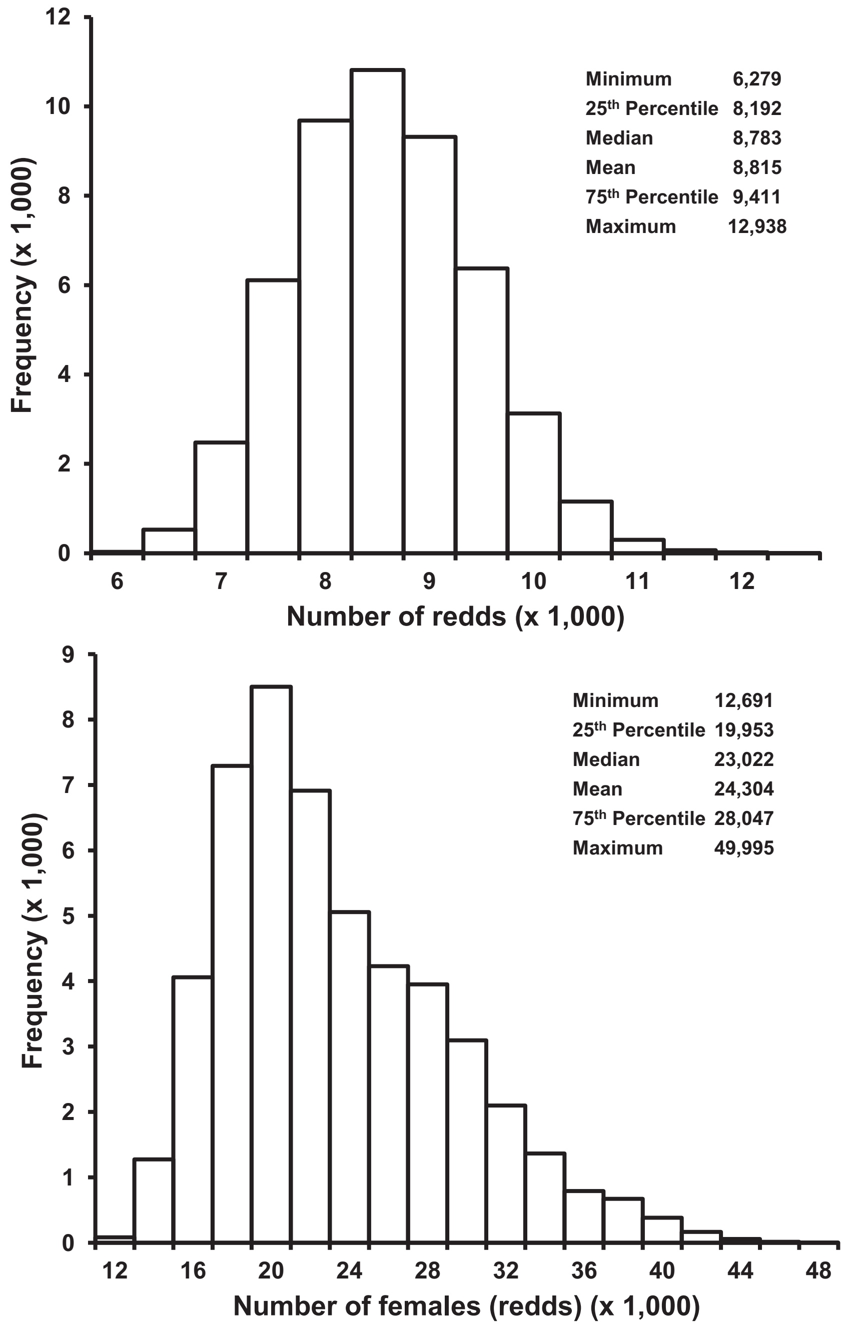
Two lines of evidence suggest that a production potential of 24 000 redds is a conservative estimate.

First, several factors suggest that the temporally and spatially adjusted archival, maximum redd counts likely underestimated the actual maximum numbers of redds.

(*a*) Although early biologists attempted to validate redd counts by comparing observation methods (e.g., Metsker 1958), their goal was to monitor population trends, not census every redd (Hassemer 1993).

(*b*) Challenging mountain flying conditions for fixed-wing aircraft within diverse watersheds and terrain, coupled with highly variable weather conditions, likely resulted in omissions of redds

Fig. 3. (top) Distribution of the bootstrapped, maximum redd potential in the Middle Fork Salmon River drainage in the 1950s–1960s if all potential spawning areas had been surveyed after all redds were constructed, with measures of central tendency and selected quantiles, and (bottom) distribution of the bootstrapped, maximum number of female Chinook salmon destined for the Middle Fork Salmon River drainage in the 1950s–1960s provided no freshwater harvest had occurred in Idaho or the Snake or Columbia rivers, with measures of central tendency and selected quantiles.



in the 1950s–1960s. For example, a Loon Creek survey during "poor" flying conditions omitted 87 (45%) of the 193 redds observed 2 days later during "improved" flying conditions (Richards and Gebhards 1959). Archival observers also reported that they likely missed redds obscured by shadows (Richards and Gebhards 1959). Visser et al. (2002) reported that helicopters maintain position at slower air speeds, allowing for more accurate counts compared with counts from fixed-wing aircraft.

(*c*) Higher redd densities in the 1950s–1960s resulted in more frequent redd clustering. Increasing redd density and presence of older redds increased counting errors (Gallagher et al. 2010), and errors of omission increased as the number and density of redd clusters increased (Visser et al. 2002). Within the MFSR, errors of omission similarly increased at higher redd densities when clustered redds were more difficult to distinguish (Thurow and McGrath 2010). Such omissions would cause us to underestimate potential, historical numbers of redds.

(*d*) Much larger salmon populations in the 1950s–1960s likely supported a more diverse age structure and may have resulted in broader spawn timing, both temporally and spatially, than we have observed since 1995. Higher adult abundances can increase age diversity, resulting in broader spawning caused by a larger number of age classes initiating spawning at different times and across more extensive spawning areas (e.g., Marteinsdottir and Thorarinsson 1998). In 2003, larger Chinook salmon escapements (2271 redds, compared with a 24-year mean of 771 redds) resulted in salmon constructing redds at lower elevations and several weeks later compared with years with smaller escapements. Broader historical spawn timing would have increased the likelihood that archival, maximum counts underestimated redds because early redds were unobservable or obscured by later redds and the latest redds were not surveyed.

(*e*) Anecdotal records suggest that three additional tributaries (Little Loon, Sheep, and Wilson creeks) formerly supported redds. No redds have been detected in these three streams since 1995, so we did not estimate their production potential, resulting in a more conservative basin-wide production potential.

Second, evidence suggests that Chinook salmon returns to the MFSR were much larger prior to the 1950s. We believe that the estimate of 24 000 redds offers a conservative, minimum historical estimate of potential. Chinook salmon harvest data reported by Lichatowich and Mobrand (1995) for spring–summer Chinook salmon in the Columbia River illustrate that abundances in the 1950s–1960s may have been about 30% of returns in the 1870s–1880s. If that ratio is accurate for MFSR stocks, MFSR salmon returns in the 1870s may have resulted in closer to 80 000 redds (24 000/0.3). The number of redds that a stream can support depends on the amount of suitable spawning habitat and the area required per spawning pair (Bjornn and Reiser 1991). In the 1940s, biologists measured and mapped the total surface area of suitable Chinook salmon spawning habitat within the MFSR drainage and estimated that its suitable spawning habitat could support 92 000 redds (Parkhurst 1941; Gebhards 1959). Consequently, although actual, historical salmon production potential in the MFSR is not known precisely, evidence suggests that the ecological escapement objective of 43 000 redds (NPT 2013) is achievable.

The MFSR's intact natal habitat and locally adapted salmon also contribute to the likelihood that the basin can achieve historical production potential. Chapman (1940) surveyed MFSR natal habitats and wrote: "The Middle Fork of the Salmon possesses immense spawning areas for spring chinook which to my knowledge are not surpassed or even reached in quantity or quality any place else in the Columbia River drainage." In contrast to many watersheds (e.g., Gayeski et al. 2011), natal salmon habitats in the MFSR remain diverse, high in quality, and connected (Thurow 2000, 2015; NMFS 2017). Such large, well-connected, high-elevation, aquatic habitats may also serve as anchors for species survival and recovery in the era of climate change (e.g., Martin and Glick 2008). Isaak et al. (2016) reported that the relatively slow pace of water temperature increases in high-elevation mountain streams portends their role as refugia for cold-water biodiversity. The MFSR's importance as a coldwater refugium is further enhanced by its unique salmon that spawn at one of the highest elevations of any spring–summer Chinook salmon population in the world (Crozier et al. 2008).

MFSR salmon stocks also retain high life history diversity, which tends to increase production and buffer population fluctuations (Greene et al. 2010; Healey 2009). Multiple freshwater and saltwater ages have the potential to provide up to 18 different age classes spawning in a single year (Gebhards 1960; James et al. 1998; Copeland and Venditti 2009). Such biocomplexity maintains diverse life history portfolios and genetic diversity that are crucial for resilience (Battin et al. 2007, Greene et al. 2010; Haak and Williams 2012). MFSR salmon populations retained both within- and across-tributary genetic population differentiation (Neville et al. 2007). These contemporary conditions increase the likelihood that historical production potential remains achievable in the MFSR, provided key factors outside the MFSR basin sustain adequate survival of migrants.

Shifting baselines and salmon management

Most North American native fish stocks have declined since Euro-American settlement, and Pauly (1995) suggested that the SBS may cause each new generation of scientists to accept, as a baseline, the stock size and species composition that occurred during their careers. With each generation, the expectation of ecological conditions shifts downward and standards are lowered, resulting in a gradual shift of the baseline, an unconscious acceptance of the disappearing resource, and the establishment of inappropriately low reference points for establishing rehabilitation targets and for evaluating species responses to management actions (Pauly 1995).

Lichatowich and Williams (2015) illustrated how the SBS applies to Chinook salmon populations in the CRB. The authors reported a lack of awareness of historical abundances; scant understanding of production potential and, in some cases, refusal to believe natural production potential; the establishment of management goals that do not account for true population potential; and the application of current population status to incorrectly measure progress toward recovery. As a result, even modest increases in salmon returns are incorrectly interpreted as "record runs" despite being far below historical abundances (Lichatowich and Williams 2015). In 2010, *The Sunday Oregonian* reported that this "could be the largest spring Chinook run on record in the Columbia River", based on a forecast of 470 000 spring Chinook salmon (Lichatowich and Williams 2015). Historical Columbia River spring Chinook salmon maximum harvests ranged from 1.7 to 2.3 million fish and the 2010 return clearly did not approach a record (Lichatowich and Williams 2015). Shifting baselines may also hide the magnitude of salmon population declines and promote the belief that natural production cannot sustain harvest levels, resulting in flawed conceptual foundations for future management (Lichatowich et al. 2017).

To overcome the SBS, Pauly (1995) recommended a framework to maximize use of accurate historical information. Jackson and Alexander (2011) similarly suggested that understanding the concept of shifting baselines helps neutralize denial of ecological changes. If ecological potential is understood, the baseline may be shifted back upward to approach actual ecological potential (Pauly 1995). Unfortunately, reliable historical datasets that might serve as more accurate baselines are often unavailable (Lichatowich et al. 2017). Here we have presented an example of how contemporary and archival, long-term datasets can be applied to repress the SBS. Below, we examine historical CRB salmon abundance estimates to provide a larger context for our work.

Columbia River Basin historical anadromous fish abundances

Historically, the Columbia River Basin supported the world's largest runs of Chinook salmon (Van Hyning 1973). The basin also supported very large populations of summer steelhead (*Oncorhynchus mykiss*), sockeye salmon (*Oncorhynchus nerka*), and coho salmon (*Oncorhynchus kisutch*), as well as runs of pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon. Nehlsen et al. (1991) estimated that over 200 distinct stocks of anadromous fish persisted in the CRB.

Estimates of the total, annual adult salmon and steelhead abundances in the CRB during the predevelopment period (prior to 1850) have ranged from 6.2 million fish (PFMC 1979) to 7.5–8.9 million (Chapman 1986) to 10–16 million (NWPPC 1986). Estimates of predevelopment fish abundance are typically based on several major assumptions and approaches: (*i*) expanded commercial landings, (*ii*) daily salmon consumption by Native Americans prior to 1800, (*iii*) consideration of ocean harvests of Chinook and coho salmon, and (*iv*) habitat-based estimates of potential salmon production (Independent Scientific Advisory Board (ISAB) 2015). Most predevelopment estimates of abundance reportedly represent the period prior to 1850 when there was relatively little habitat degradation (NWPPC 1986), even though the harvest-based values reflect the period of large catches from 1880 to 1928 (ISAB 2015). ISAB (2015) reported that "limited data" suggested that the potential capacity was likely in the range of 5 to 9 million adult fish per year and the "primary evidence" (i.e., probable harvest rates) supported an estimate of around 6 million fish per year, based on harvests during a period of favorable ocean conditions in the late 1800s to early 1900s (ISAB 2015).

The predevelopment CRB probably produced more Chinook salmon and steelhead than any other watershed worldwide, along with relatively large numbers of coho salmon (ISAB 2015). These very large historical abundances were reflected in a commercial harvest of 2.3 million Chinook salmon (all three races with summer-run fish dominant) in the mainstem Columbia River in 1883 (Mullan et al. 1992). This estimate did not include tribal or sport harvest in the mainstem Columbia River or any harvest in tributaries, including such large basins as the Snake, Willamette, or Yakima rivers. Across the North Pacific, pink, chum, and sockeye salmon are much more abundant than Chinook and coho salmon and steelhead (Ruggerone et al. 2010). Despite being at or near the southern-most range of these more abundant salmon species, the CRB is the third largest salmon-bearing watershed flowing into the North Pacific Ocean (after the Amur and Yukon rivers) (ISAB 2015). Today, most wild CRB chum, pink, and coho salmon stocks are extinct (Williams 2006). Although these historical abundance estimates provide important insights into overall CRB salmon production potential, they are too broad in scale to assist in the establishment of finer scale management goals. In comparison, our results are relevant at the finer scale of ESA listed salmon stocks in the Snake River basin. Our approach is also applicable to other basins.

Comparison of archival and contemporary MFSR Chinook salmon abundance

The 60-year record of IDFG archival redd counts provides a unique opportunity to examine time trends in Chinook salmon abundance within the mainstem MFSR and six tributaries. The total number of redds observed annually in the archival index areas ranged from 3102 in 1957 to 14 in 1995. Prior to 1971, on average, 2089 redds were observed; after 1970, on average, 546 redds were observed. In the 1990s, on average, 228 redds were counted, and fewer than 85 redds were observed during 4 years in that decade. Although this long-term database is invaluable for monitoring population trends, it is biased low and does not enable managers to accurately assess total escapements or actual production potential (see online Supplementary material, Fig. S3[1]).

In response to the need for more complete redd estimates, RMRS has counted redds continuously since 1995 and consistently and annually censused all potential spawning areas within the MFSR drainage. Total redd counts ranged from 20 in 1995 to 2271 in 2003. Although continuous counts provide an estimate of recent population abundances, they fail to estimate actual production potential. In contrast to our estimated 1950s–1960s production potential of 24 000 redds, contemporary continuous surveys have observed an average of 771 redds during the past 24 years (1995–2018), 3.2% of the production potential.

Snake River basin Chinook salmon recovery and management goals

Recovery plans (e.g., NMFS 2017) identify actions needed to restore threatened and endangered species to a self-sustaining level at which ESA protections are no longer need. The requirement for determining when a species no longer requires ESA protection and may be delisted is when "the species is no longer in danger of extinction or not likely to become endangered within the foreseeable future, based on evaluation of the listing factors specified in ESA section 4(a)(1)." Consequently, to remove the Snake River spring–summer Chinook salmon "evolutionarily significant unit" (ESU) from the Federal List of Endangered and Threatened Wildlife and Plants, NMFS must determine that the ESU, as evaluated under ESA listing factors, is no longer likely to become endangered (NMFS 2017). Within the Snake River basin, management goals for spring–summer Chinook salmon are focused at smaller scales ranging from the "major population group" (MPG) to ESU levels. In many cases, populations are also managed at the local population scale. Unfortunately, even the finest scale management plans rarely reference historical data.

Beyond ESA requirements, a much more challenging management objective is to increase wild salmon populations to levels that would sustain harvest (Lackey 2017) and other ecological benefits. Components of the ESA recovery goals rely heavily on biological viability criteria (NMFS 2017). Extended "broad sense" goals exceed requirements for delisting under the ESA recovery plan to address additional legislative mandates and values (NMFS 2017). Most planning entities and citizen groups agree that while delisting salmon is an important goal, ultimately the "broad sense" goal is to restore thriving, abundant fish populations that provide ecological, social, cultural, recreational, and economic benefits in perpetuity for all citizens, as well as sufficient harvest to meet federal treaty obligations (NMFS 2017). Idaho Code 36-103, for example, defines the IDFG Mission to "preserve, protect, perpetuate and manage all wildlife, including wild animals, wild birds, and fish within the state of Idaho" to provide continued supplies for the citizens of the state. Hence, Idaho's salmon management goals for the MFSR far exceed ESA's de-listing requirements.

Factors affecting contemporary MFSR Chinook salmon production

Despite the MFSR's intact habitat, large size, operating landscape processes, and genetically plus phenotypically diverse indigenous salmon stocks, several factors may affect contemporary production potential: changes in population synchrony, reduced marine-derived nutrients, variable marine survival, and changes in smolt-to-adult survival. The key limiting factors affecting these populations are primarily from outside the natal habitat (NMFS 2017).

Population synchrony

Metapopulation dynamics (Hanski 1998) may affect future production potential because salmon populations exhibit a degree of synchrony, or correlation, among populations (Harrison and Taylor 1996). Isaak et al. (2003) evaluated synchrony among MFSR Chinook salmon populations and reported historically low levels of synchrony among tested populations that resulted in a high level of stability and resilience. Consequently, not all future populations would be expected to achieve maximum levels of abundance at the same time. However, after undergoing a six-fold reduction in abundance since the mid-1970s, the MFSR transitioned to a state in which population stability appeared greatly reduced, correlations among populations increased, and the range of inter-series correlations narrowed (Isaak et al. 2003). Under these conditions, multiple simultaneous extirpations could occur and have detrimental consequences for metapopulation persistence. As described in the Migration corridor section, salmon population declines were coincident with reduced SARs (smolt-to-adult return rates) between 1961 and 1975 that were also coincident with observed increases in synchrony.

Marine-derived nutrients

Reductions in the availability of marine-derived nutrients in natal habitats might limit future MFSR salmon populations. Marine carbon and nitrogen deposited by adult salmon is sequestered at multiple trophic levels in freshwater and terrestrial systems; these subsidies often dramatically influence community productivity and demographics (Wipfli and Baxter 2010). Biofilm mass and invertebrate density increased up to 25 times in Alaskan streams with spawning salmon; more salmon led to increased responses, up to a threshold (Wipfli et al. 1999). Because contemporary salmon returns to the MFSR are averaging 3%–4% of the 1950s–1960s abundances, evidence suggests that marine-derived nutrients have also dramatically declined.

However, several gaps exist in the empirical science of nutrients and salmon production (Collins et al. 2015). For example, studies in northwestern river basins reported that despite reduced contemporary anadromous fish populations, invertebrate production generally exceeded fish demand (Bellmore et al. 2012, 2013). Collins et al. (2015) warned that an overemphasis on the ecological effects of salmon-derived nutrients and the focus on a salmon nutrient enrichment paradigm as a recovery strategy provide an incomplete solution to a complex problem and may divert attention from larger impediments limiting salmon populations.

Ocean regimes

Transitions from one climatic state to another are called regime shifts, and there is substantial literature linking shifts in ocean condition to the distribution and abundance of aquatic organisms (Nielsen and Ruggerone 2009), including salmon. Consequently, full MFSR production potential will only be achieved during favorable ocean regimes. Changes in ocean food-web structure, associated with long-term warming trends and climatic PDO regime shifts, may have influenced the availability of forage fishes and reduced Chinook salmon growth and age at maturity (Lewis et al. 2015). Ocean conditions are not as favorable for wild salmon as in the past; a changing climate and increasing hatchery salmon releases may limit future ocean production of wild fish (Ruggerone and Irvine 2018).

Migration corridor conditions

Construction and operation of mainstem dams on the Columbia and Snake rivers are considered the proximate cause of Snake River anadromous fish declines (CBFWA 1990; Thurow et al. 2000): "Federal hydropower projects in the lower Columbia and Snake Rivers remain a primary threat to the viability of Snake River spring–summer Chinook salmon and steelhead" (NMFS 2017). U.S. District Court Judge Simon stated that Federal policy is not "trending toward recovery" and "Federal dams are causing continued irreparable harm to imperiled salmon and steelhead." (Simon 2016).

Adverse effects of mainstem dams and impoundments on salmon and steelhead survival are well documented (Raymond 1979). Dam construction converted 523 km of free-flowing rivers to reservoirs. These impoundments increased water travel times from the Snake River to the Bonneville Dam from an average of 2 days before the dam to 19 days after the dam and delayed arrival to the estuary by up to 6 weeks (Tuomikoski et al. 2009; Petrosky and Schaller 2010). Additional changes in the migration corridor included increasing water temperatures, higher vulnerability to native and introduced predators, and poorer food availability reflected in reduced juvenile growth (Schaller et al. 1999; Budy et al. 2002; Tiffan et al. 2014).

As a result of these changes, SARs declined from 3.5%–6% in the 1960s (Raymond 1988) to a mean of 0.7% from 2000 to 2017 (McCann et al. 2019). Snake River stocks above eight dams survive one-quarter to one-third as well as stocks above three dams (Schaller et al. 1999, 2014; Deriso et al. 2001; Schaller and Petrosky 2007). The Northwest Power and Conservation Council recovery target to achieve viable population status is a mean SAR of 4% with a range from 2% to 6% (NPCC 2009, 2014). MFSR Chinook salmon populations will not achieve their production potential until SAR goals are achieved.

Framework for sustainable management

What is the pragmatic value of our analysis of maximum production potential? Our answer: we provide a maximum estimate of the upper range of the system's population performance that is possible under near-optimal conditions. Nonetheless, it is instructive to compare maximum production potential with contemporary management goals. In spirit, maximum production potential helps inform goals for re-establishing the full range of ecological services that depend on salmon as a keystone species (Willson and Halupka 1995) and on their delivery of marine-derived nutrients. Spawning escapements must likely approach maximum potential to fully charge the system with nutrients. Because maximum production inevitably preceded historical exploitation and empirical abundance estimates, maximum levels will need to be estimated from available data (Thurstan et al. 2015). By definition, sustainable fishery goals will tend to be below the maximum and within a domain of relative stability. A comparison of maximum potential with current management goals provides an indication of what could be achieved by the salmon population and whether alternative management goals are feasible. For example, our approach could also incorporate a mean or median abundance from a period judged to have lower, sustainable exploitation. Finally, viability goals are often based on observed historical abundances, which may be far less than potential maximum abundances. Contrasting viability goals with maximum production potential offers examination of the magnitude of changes that have degraded system potential. Such comparisons provide a robust framework and a new reference point and perspective for managers to consider when developing sustainable goals.

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References

Battin, J., Wiley, M.W., Ruckelshaus, M.H., Palmer, R.N., Korb, E., Bartz, K.K., and Imaki, H. 2007. Projected impacts of climate change on salmon habitat restoration. Proc. Natl. Acad. Sci. **104**: 6720–6725. doi:10.1073/pnas.0701685104. PMID:17412830.

Bellmore, J.R., Baxter, C.V., Ray, A.M., Denny, L., Tardy, K., and Galloway, E. 2012. Assessing the potential for salmon recovery via floodplain restoration: a multitrophic level comparison of dredge-mined to reference segments. Environ. Manage. **49**: 734–750. doi:10.1007/s00267-012-9813-x. PMID:22323109.

Bellmore, J.R., Baxter, C.V., Martens, K., and Connolly, P.J. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. Ecol. Appl. **23**: 189–207. doi:10.1890/12-0806.1. PMID:23495646.

Bjornn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. Am. Fish. Soc. Spec. Publ. **19**: 138.

Budy, P., Thiede, G.P., Bouwes, N., Petrosky, C.E., and Schaller, H. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. N. Am. J. Fish. Manage. **22**: 35–51. doi:10.1577/1548-8675(2002)022<0035:ELDMOS>2.0.CO;2.

Burner, C.J. 1951. Characteristics of spawning nests of Columbia River salmon. Fish. Bull. Fish Wildl. Serv. **52**: 97–110.

Chapman, D.W. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. Trans. Am. Fish. Soc. **115**: 662–670. doi:10.1577/1548-8659(1986)115<662:SASAIT>2.0.CO;2.

Chapman, W.M. 1940. Report of a field trip to the Snake River drainage in Idaho and eastern Oregon, 1940. Washington Department of Fisheries, Olympia, Wash.

Claro, R., de Mitcheson, Y.S., Lindeman, K.C., and García-Cagide, A.R. 2009. Historical analysis of Cuban commercial fishing effort and the effects of management interventions on important reef fishes from 1960–2005. Fish. Res. **99**: 7–16. doi:10.1016/j.fishres.2009.04.004.

Collins, S.F., Marcarelli, A.M., Baxter, C.V., and Wipfli, M.S. 2015. A critical assessment of the ecological assumptions underpinning compensatory mitigation of salmon-derived nutrients. Environ. Manage. **56**: 571–586. doi:10.1007/s00267-015-0538-5. PMID:25968140.

Columbia Basin Fish and Wildlife Authority (CBFWA). 1990. Integrated system plan for salmon and steelhead production in the Columbia Basin. Northwest Power Planning Council, Portland, Ore.

Copeland, T., and Venditti, D.A. 2009. Contribution of three life history types to smolt production in a Chinook salmon (*Oncorhynchus tshawytscha*) population. Can. J. Fish. Aquat. Sci. **66**(10): 1658–1665. doi:10.1139/F09-110.

Courbois, J.Y., Katz, S.L., Isaak, D.J., Steel, E.A., Thurow, R.F., Wargo Rub, A.M., and Jordan, C.E. 2008. Evaluating probability sampling strategies for estimating redd counts: an example with Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **65**(9): 1814–1830. doi:10.1139/F08-092.

Crisp, D.T., and Carling, P.A. 1989. Observations on siting, dimensions and structure of salmonid redds. J. Fish Biol. **34**: 119–134. doi:10.1111/j.1095-8649.1989.tb02962.x.

Crozier, L.G., Hendry, A.P., Lawson, P.W., Quinn, T.P., Mantua, N.J., Battin, J., et al. 2008. Potential responses to climate change in organisms with complex life histories: Evolution and plasticity in Pacific salmon. Evol. Appl. **1**: 252–270. doi:10.1111/j.1752-4571.2008.00033.x. PMID:25567630.

Deriso, R.B., Marmorek, D.R., and Parnell, I.J. 2001. Retrospective patterns of differential mortality and common year-effects experienced by spring and summer chinook salmon (*Oncorhynchus tshawytscha*) of the Columbia River. Can. J. Fish. Aquat. Sci. **58**(12): 2419–2430. doi:10.1139/f01-172.

Dunham, J., Rieman, B., and Davis, K. 2001. Sources and magnitude of sampling error in redd counts for bull trout. N. Am. J. Fish. Manage. **21**: 343–352. doi:10.1577/1548-8675(2001)021<0343:SAMOSE>2.0.CO;2.

Elms-Cockrum, T.J. 2001. 1999 Salmon Spawning Ground Surveys. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Res01-10Elms-Cockrum1999%20Salmon%20Spawning%20Ground%20Surveys.pdf [accessed September 2018].

Emlen, J.M. 1995. Population viability of the Snake River chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **52**(7): 1442–1448. doi:10.1139/f95-139.

Fullerton, A.H., Anzalone, S., Moran, P., Van Doornik, D.M., Copeland, T., and Zabel, R.W. 2016. Setting spatial conservation priorities despite incomplete data for characterizing metapopulations. Ecol. Appl. **26**: 2560–2580. doi:10.1002/eap.1411.

Gallagher, S.P., and Gallagher, C.M. 2005. Discrimination of Chinook salmon, coho salmon, and steelhead redds and evaluation of the use of redd data for estimating escapement in several unregulated streams in northern California. N. Am. J. Fish. Manage. **25**: 284–300. doi:10.1577/M04-016.1.

Gallagher, S.P., Adams, P.B., Wright, D.W., and Collins, B.W. 2010. Performance of spawner survey techniques at low abundance levels. N. Am. J. Fish. Manage. **30**: 1086–1097. doi:10.1577/M09-204.1.

Gayeski, N., McMillan, B., and Trotter, P. 2011. Historical abundance of Puget Sound steelhead, *Oncorhynchus mykiss*, estimated from catch record data. Can. J. Fish. Aquat. Sci. **68**(3): 498–510. doi:10.1139/F10-166.

Gebhards, S.V. 1959. Preliminary planning report — Salmon River. Columbia River Fisheries Development Program. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Res-Gebhards1958%20Planning%20Report%20-%20Salmon%20River.pdf [accessed September 2018].

Gebhards, S.V. 1960. Biological notes on precocious male Chinook salmon parr in the Salmon River drainage, Idaho. Progr. Fish-Cult. **22**: 121–123. doi:10.1577/1548-8659(1960)22[121:BNOPMC]2.0.CO;2.

Greene, C.M., Hall, J.E., Guilbault, K.R., and Quinn, T.P. 2010. Improved viability of populations with diverse life-history portfolios. Biol. Lett. **6**: 382–386. doi:10.1098/rsbl.2009.0780. PMID:20007162.

Haak, A.L., and Williams, J.E. 2012. Spreading the risk: native trout management in a warmer and less-certain future. N. Am. J. Fish. Manage. **32**: 387–401. doi:10.1080/02755947.2012.678963.

Hanski, I. 1998. Metapopulation dynamics. Nature, **396**: 41. doi:10.1038/23876.

Harrison, S., and Taylor, A.D. 1996. Empirical evidence for metapopulation dynamics. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* I.A. Hanski and M.E. Gilpin. Academic Press, New York. pp. 27–39.

Hassemer, P.F. 1993. Salmon spawning ground surveys, 1989–92. Pacific Salmon Treaty Program Award Number NA17FP0168-02, Idaho Fish Game Rep. 01-10, Boise, Ida. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Res-Hassemer1992%20Salmon%20Spawning%20Ground%20Surveys.pdf [accessed September 2018].

Hauck, F.R. 1951. Aerial survey of Chinook salmon spawning: Utilization of the major streams of the Salmon River drainage. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Mgt-Hauck1951%20Aerial%20Survey%20of%20Chinook%20Salmon%20Spawing%20Utilization%20of%20the%20Major%20Streams%20of%20the%20Salmon%20River%20Drainage.pdf [accessed September 2018].

Hauck, F.R. 1952*a*. A survey of the spring Chinook salmon spawning utilization of Idaho streams. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Res-Hauck1952%20Survey%20of%20the%20Spring%20Salmon%20Spawning%20Utilization%20of%20Idaho%20Streams.pdf [accessed October 2018].

Hauck, F.R. 1952*b*. The spring Chinook sport fishery in Idaho, 1952. Completion Report. Project F1-R-2. IDFG, Boise. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Mgt-Hauck1952%20Spring%20Chinook%20Sport%20Fishery%20in%20Idaho.pdf [accessed October 2018].

Hauck, F.R. 1953. The size and timing of runs of anadromous species of fish in the Idaho tributaries of the Columbia River. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Res-Hauck1953%20Size%20and%20Timing%20of%20Runs%20of%20Anadromous%20Species%20of%20Fish%20in%20the%20Idaho%20Tributaries%20of%20the%20Columbia%20River.pdf [accessed October 2018].

Hauck, F.R. 1954. Spring Chinook salmon in Idaho waters. Completion Report. Project F 1-R-3. IDFG, Boise, Ida. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Mgt-Hauck1954%20Spring%20Chinook%20Salmon%20in%20Idaho%20Waters.pdf [accessed October 2018].

Healey, M.C. 2009. Resilient salmon, resilient fisheries for British Columbia, Canada. Ecol. Soc. **14**(1): 2. [Online.] Available from http://www.ecologyandsociety.org/vol14/iss1/art2/ [accessed October 2018].

Humphries, P., and Winemiller, K.O. 2009. Historical impacts on river fauna, shifting baselines, and challenges for restoration. BioScience, **59**: 673–684. doi:10.1525/bio.2009.59.8.9.

Idaho Department of Fish and Game (IDFG). 1954. The size and timing of anadromous species of fish in the Columbia and Snake Rivers and their tributaries above the confluence of the Snake River. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Res-IDFG1954%20Size%20and%20Timing%20of%20Runs%20of%20Anadromous%20Species%20of%20Fish%20in%20the%20Columbia%20and%20Snake%20River%20and%20their%20Tributaries.pdf [accessed October 2018].

Idaho Department of Fish and Game (IDFG). 1955. The size and timing of runs of adult spring Chinook salmon in the Columbia and Snake Rivers and their tributaries above the confluence of the Snake River. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Res-IDFG1955%20Size%20and%20Timing%20of%20Runs%20of%20Adult%20Spring%20Chinook%20Salmon%20in%20the%20Columbia%20and%20Snake%20Rivers%20and%20their%20Tributaries.pdf [accessed October 2018].

Idaho Department of Fish and Game (IDFG). 1992. Anadromous Fish Management Plan 1992–1996. IDFG, Boise, Ida. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Mgt-1992-1996Anadromous%20Fish%20Management.pdf [accessed October 2018].

Idaho Department of Fish and Game (IDFG). 2019. Fisheries Management Plan, 2019–2024. IDFG, Boise, Ida. [Online.] Available from https://idfg.idaho.gov/sites/default/files/2019-2024-idaho-fisheries-management-plan-original.pdf [accessed March 2019].

Independent Scientific Advisory Board (ISAB). 2015. Density dependence and its implications for fish management and restoration programs in the Columbia River. Northwest Power and Conservation Council, Portland, Oregon. ISAB Report 2015-1. [Online.] Available from www.nwcouncil.org/fw/isab/isab2015-1 [accessed September 2018].

Isaak, D.J., and Thurow, R.F. 2006. Network-scale spatial and temporal variation in Chinook salmon (*Oncorhynchus tshawytscha*) redd distributions: patterns inferred from spatially continuous replicate surveys. Can. J. Fish. Aquat. Sci. **63**(2): 285–296. doi:10.1139/f05-214.

Isaak, D.J., Thurow, R.F., Rieman, B.E., and Dunham, J.B. 2003. Temporal variation in synchrony among chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho. Can. J. Fish. Aquat. Sci. **60**(7): 840–848. doi:10.1139/f03-073.

Isaak, D.J., Young, M.K., Luce, C.H., Hostetler, S.W., Wenger, S.J., Peterson, E.E., Ver Hoef, J.M., et al. 2016. Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. Proc. Natl. Acad. Sci. U.S.A. **113**: 4374–4379. doi:10.1073/pnas.1522429113. PMID:27044091.

Jackson, J.B., and Alexander, K.E. 2011. Introduction: the importance of shifting baselines. *In* Shifting baselines. The past and the future of ocean fisheries. *Edited by* J.B.C. Jackson, K.E. Alexander, and E. Sala. Island Press, Washington, D.C. pp. 1–7.

James, B.B., Pearsons, T.N., and McMicheal, G.A. 1998. Washington Department of Fish and Wildlife, Spring Chinook salmon interactions indices and residual/precocial monitoring in the Upper Yakima basin. Annual Report to Bonneville Power Administration, Contract No. 1995B164878, Project No. 0906409, BPA Report DOE/BP-64878-4.

Joint Staff Report. 2019. Stock status and fisheries for spring Chinook, summer Chinook, sockeye, steelhead, and other species. Joint Columbia River Management Staff, Oregon Department of Fish & Wildlife and Washington Department of Fish & Wildlife.

King, J., and Thurow, R. 2000. Sediment monitoring techniques validation. Completion Report. *Prepared for* Idaho Department of Health and Welfare, Division of Environmental Quality. USDA Forest Service, Intermountain Research Station, Boise, Ida.

Lackey, R.T. 2017. Science and salmon recovery. *In* New strategies for wicked problems: science and solutions in the 21st century. *Edited by* E.P. Weber, D.H. Lach, and B.S. Steel. Oregon State University Press, Corvallis, Ore. pp. 69–94.

Lee, D.C., Sedell, J.R., Rieman, B.E., Thurow, R.F., and Williams, J.E. 1997. Broadscale assessment of aquatic species and habitats. Chapter 4. *In* An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins. Vol. 1. *Edited by* T.M. Quigley and S.J. Arbelbide. USDA Forest Service, Pacific Northwest Research Station, Portland, Ore., Gen. Tech. Rep. PNW-GTR-405. pp. 1058–1496.

Lewis, B., Grant, W.S., Brenner, R.E., and Hamazaki, T. 2015. Changes in size and age of Chinook salmon *Oncorhynchus tshawytscha* returning to Alaska. PLoS ONE, **10**(6): e0130184. doi:10.1371/journal.pone.0130184. PMID:26090990.

Lichatowich, J.A., and Mobrand, L.E. 1995. Analysis of Chinook salmon in the Columbia River from an ecosystem perspective. *Prepared for* Bonneville Power Administration. Available from https://www.cbfish.org/Document.mvc/DocumentViewer/25105-2/h25105-2.pdf.

Lichatowich, J., and Williams, R. 2015. Faith in nature: The missing element in salmon management and mitigation programs. The Osprey, Issue No. 81. [Online.] Available from www.flyfishersinternational.org [accessed October 2018].

Lichatowich, J., Williams, R., Bakke, B., Myron, J., Bella, D., McMillan, B., and Montgomery, D. 2017. Wild Pacific salmon: a threatened legacy. Booklet funded by Fly Fishers International and Wild Fish Conservancy. Bemis Printing, St Helens, Ore.

Limburg, K.E., and Waldman, J.R. 2009. Dramatic declines in North Atlantic diadromous fishes. BioScience, **59**: 955–965. doi:10.1525/bio.2009.59.11.7.

Mallet, J. 1974. Inventory of salmon and steelhead resources, habitat, use and demands. Job Performance Report. Idaho Department of Fish and Game, Boise, Ida.

Marteinsdottir, G., and Thorarinsson, K. 1998. Improving the stock–recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. Can. J. Fish. Aquat. Sci. **55**(6): 1372–1377. doi:10.1139/f98-035.

Martin, J., and Glick, P. 2008. A Great Wave: Solutions for Columbia and Snake River salmon in the age of global warming. Report to Light in the River. [Online.] Available from https://www.nwf.org/~/media/PDFs/Global-Warming/Reports/AGreatWaveRising.pdf [accessed September 2018].

Matthews, G.M., and Waples, R.S. 1991. Status review for Snake River spring and summer chinook salmon. National Marine Fisheries Service, Seattle, Wash., NOAA Tech. Memo. NMFS F/NWC-200.

Maxell, B.A. 1999. A power analysis on the monitoring of bull trout stocks using redd counts. N. Am. J. Fish. Manage. **19**: 860–866. doi:10.1577/1548-8675(1999)019<0860:APAOTM>2.0.CO;2.

McCann, J., Chockley, B., Cooper, E., Hsu, B., Scheer, G., Haeseker, S., Lessard, R., Copeland, T., Tinus, E., Storch, A., and Rawding, D. 2019. Comparative survival study of PIT-tagged spring/summer/fall Chinook, summer steelhead, and sockeye. 2019 Annual Report, BPA Contract 19960200. [Online.] Available from http://www.fpc.org/documents/CSS/2019CSSAnnualReport.pdf [accessed January 2020].

Metsker, H.E. 1958. Aerial survey of spring Chinook salmon redds in the Salmon and Weiser River drainages. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Mgt-Metsker1958%20Aerial%20Survey%20of%20Spring%20Chinook%20Salmon%20Redds%20in%20the%20Salmon%20and%20Weiser%20River%20Drainages.pdf [accessed September 2018].

Minshall, G.W., Brock, J.T., and Andrews, D.A. 1981. Biological, water quality and aquatic habitat response to wildfire in the Middle Fork of the Salmon River and its tributaries. Idaho State University, Pocatello, Ida.

Mullan. J.W., Williams, K.R., Rhodus, G., Hillman, T.W., and McIntyre, J.D. 1992. Production and habitat of salmonids in mid-Columbia River tributary streams. U.S. Fish and Wildlife Service, Monograph 1.

Murdoch, A.R., Pearsons, T.N., and Maitland, T.W. 2009. The number of redds constructed per female spring Chinook salmon in the Wenatchee River basin. N. Am. J. Fish. Manage. **29**: 441–446. doi:10.1577/M08-063.1.

National Marine Fisheries Service (NMFS). 2000. Biological opinion of the Federal Columbia River Power System, including the juvenile fish transportation program and the Bureau of Reclamation's 31 dams including the entire Columbia basin project. NMFS, Seattle, Wash.

National Marine Fisheries Service (NMFS). 2017. ESA Recovery Plan for Snake River Spring/Summer Chinook Salmon (*Oncorhynchus tshawytscha*) & Snake River Basin Steelhead (*Oncorhynchus mykiss*). [Online.] Available from https://www.westcoast.fisheries.noaa.gov/publications/recovery_planning/salmon_steelhead/domains/interior_columbia/snake/Final%20Snake%20Recovery%20Plan%20Docs/final_snake_river_spring-summer_chinook_salmon_and_snake_river_basin_steelhead_recovery_plan.pdf [accessed September 2018].

National Research Council (NRC). 1996. Upstream: Salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C. pp. 39–66.

Nehlsen, W., Williams, J.E., and Lichatowich, J.A. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries, **16**: 4–21. doi:10.1577/1548-8446(1991)016<0004:PSATCS>2.0.CO;2.

Neville, H., Isaak, D., Thurow, R., Dunham, J., and Rieman, B. 2007. Microsatellite variation reveals weak genetic structure and retention of genetic variability in threatened Chinook salmon (*Oncorhynchus tshawytscha*) within a Snake River watershed. Conserv. Genet. **8**: 133–147. doi:10.1007/s10592-006-9155-4.

Nielsen, J.L., and Ruggerone, G.T. 2009. Climate change and a dynamic ocean carrying capacity: growth and survival of Pacific salmon at sea. *In* American Fisheries Society Symposium 71, 2008. Available from https://alaska.usgs.gov/products/pubs/2008/2008_Nielsen_Ruggerone_AFSS_71.pdf.

Nez Perce Tribe (NPT). 2013. Nez Perce Tribe Department of Fisheries Resources Management Plan 2013–2028. [Online.] Available from https://damsense.org/wp-content/uploads/2016/05/Nez-Perce-Fish-Management-Plan-2013-2028.pdf [accessed September 2018].

Northwest Power and Conservation Council (NPCC). 2009. Columbia River Basin Fish and Wildlife Program. Council Document 2009-02. [Online.] Available from https://www.nwcouncil.org/sites/default/files/2009_09F.pdf [accessed September 2018].

Northwest Power and Conservation Council (NPCC). 2014. Columbia River Basin Fish and Wildlife Program. Council Document 2014-12. [Online.] Available from http://www.nwcouncil.org/media/7148624/2014-12.pdf [accessed September 2018].

Northwest Power Planning Council (NWPPC). 1986. Council staff compilation of information on salmon and steelhead losses in the Columbia River basin. Columbia River Basin Fish and Wildlife Program, Northwest Power Planning Council, Portland, Ore. Appendix D.

Pacific Fishery Management Council (PFMC). 1979. Freshwater habitat, salmon produced, and escapements for natural spawning along the Pacific coast of the U.S. *Prepared by* the Anadromous Salmonid Environmental Task Force of the Pacific Fishery Management Council, Portland, Ore.

Parkhurst, Z.E. 1941. Survey of the Columbia River and its tributaries, part 7, area VI. Snake River from above the Grande Ronde River through the Payette River. Special Scientific Report — Fisheries No. 40, U.S. Fish and Wildlife Service.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol Evol. **10**: 430. doi:10.1016/S0169-5347(00)89171-5.

Petrosky, C.E., and Schaller, H.A. 2010. Influence of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook salmon and steelhead. Ecol. Freshw. Fish, **19**: 520–536. doi:10.1111/j.1600-0633.2010.00425.x.

Pirtle, R.B. 1956. The size and timing of runs of adult spring Chinook salmon in the Columbia and Snake Rivers and their tributaries above the confluence of the Snake River. Report to U.S. Army Corps of Engineers. Idaho Department of Fish and Game (IDFG), Boise, Ida.

Pirtle, R.B. 1958. Creel census summary fisheries management area II, District 2. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Mgt-Pirtle1958%20Creel%20Census%20Summary%20Fisheries%20Management%20Area%202.pdf [accessed September 2018].

Raymond, H.L. 1979. Effects of dams and impoundments on migrations of juvenile Chinook salmon and steelhead from the Snake River, 1966 to 1975. Trans. Am. Fish. Soc. **108**: 505–529. doi: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. N. Am. J. Fish. Manage. **8**: 1–24. doi:10.1577/1548-8675(1988)008<0001:EOHDAF>2.3.CO;2.

Richards, M., and Gebhards, S. 1959. Aerial survey of spring Chinook salmon redds in the Salmon and Weiser River drainages. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Mgt-Richards1958%20Aerial%20Survey%20of%20Spring%20Chinook%20Salmon%20Redds%20in%20the%20Salmon%20and%20Weiser%20River%20Drainages.pdf [accessed September 2018].

Rieman, B.E., and McIntyre, J.D. 1996. Spatial and temporal variability in bull trout redd counts. N. Am. J. Fish. Manage. **16**: 132–141. doi:10.1577/1548-8675(1996)016<0132:SATVIB>2.3.CO;2.

Ruggerone, G.T., and 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. Mar. Coast. Fish. **10**: 152–168. doi:10.1002/mcf2.10023.

Ruggerone, G.T., Peterman, R.M., Dorner, B., and Myers, K.W. 2010. Magnitude and trends in abundance of hatchery and wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean. Mar. Coast. Fish. **2**: 306–328. doi:10.1577/C09-054.1.

Schaller, H.A., and Petrosky, C.E. 2007. Assessing hydrosystem influence on delayed mortality of Snake River stream-type Chinook salmon. N. Am. J. Fish. Manage. **27**: 810–824. doi:10.1577/M06-083.1.

Schaller, H.A., Petrosky, C.E., and 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. Can. J. Fish. Aquat. Sci. **56**(6): 1031–1045. doi:10.1139/f99-037.

Schaller, H.A., Petrosky, C.E., and Tinus, E.S. 2014. Evaluating river management during seaward migration to recover Columbia River stream-type Chinook salmon considering the variation in marine conditions Can. J. Fish. Aquat. Sci. **71**(2): 259–271. doi:10.1139/cjfas-2013-0226.

Schoning, R.W. 1953. Snake River survey, 1952. Oregon Fish Commission Report. Research Laboratory, Clackamas, Ore.

Schwartzberg, M., and Roger, P. 1986. An Annotated Compendium of Spawning Ground Surveys in the Columbia River Basin Above Bonneville Dam, 1960–1984. Columbia River Inter-Tribal Fish Commission Technical Report 86-1, Portland, Oregon. [Online.] Available from http://www.critfc.org/wp-content/uploads/2013/05/86-1.pdf [accessed October 2018].

Servheen, G., Huntington, C., et al. 2001. Salmon subbasin summary. Prepared for the Northwest Power Planning Council. Available from http://cfw.nwcouncil.org/Content/FWProgram/ReviewCycle/fy2002ms/workplan/011130Salmon.pdf.

Simon, M.S. 2016. Opinion and order. Case No. 3:01-cv-006440-SI. [Online.] Available from https://www.documentcloud.org/documents/2823619-1404-2065-Opinion-and-Order.html [accessed October 2018].

Soga, M., and Gaston, K.J. 2018. Shifting baseline syndrome: causes, consequences, and implications. Front. Ecol. Environ. **16**: 222–230. doi:10.1002/fee.1794.

Stiefel, C., Barnett, B., Wright, K.K., Apperson, K.A., Belnap, M., Hand, R., et al. 2016. Adult Chinook salmon monitoring. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Res16-12Stiefel2015%20Adult%20Chinook%20Salmon%20Monitoring.pdf [accessed September 2018].

Thompson, S.K. 1992. Sampling. Wiley, New York.

Thurow, R.F. 1985. Middle Fork Salmon River fisheries investigations. Federal Aid in Fish Restoration Project F-73-R-6, Idaho Department of Fish and Game, JobCompletionReport,Boise,Ida.[Online.]Availablefromhttps://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Res-Thurow1984%20River%20and%20Stream%20Investigations%20Middle%20Fork%20Salmon%20River.pdf [accessed September 2018].

Thurow, R.F. 2000. Dynamics of Chinook salmon populations within Idaho's Frank Church wilderness: implications for persistence. *In* Wilderness Science in a Time of Change Conference. *Edited by* S.F. McCool, D.N. Cole, W.T. Borrie, and J. O'Loughlin. USDA For. Ser., RMRS-P-15-VOL-3. pp. 143–151.

Thurow, R.F. 2015. Salmon, landscapes, and functioning ecosystems: a wilderness lesson in mutual dependency. U.S. Department of Agriculture, Forest Service. Wag Tales-Newsletter of the Chief's Wilderness Advisory Group. [Online.] Available from http://fsweb.wo.fs.fed.us/rhwr/wilderness/wag/index_wag.html [accessed October 2018].

Thurow, R.F., and McGrath, C.C. 2010. Evaluating the bias and precision of Chinook salmon redd counts in the Middle Fork Salmon River basin, Idaho. Annual Report for BPA Project Number 2002-049-00, Contract 48835. *Prepared for* U.S. Department of Energy Bonneville Power Administration, Portland, Ore.

Thurow, R.F., Lee, D.C., and Rieman, B.E. 2000. Status and distribution of Chinook salmon and steelhead in the interior Columbia River basin and portions of the Klamath River basin. *In* Sustainable fisheries management: Pacific salmon. *Edited by* E. Knudsen, C. Steward, D. MacDonald, J. Williams, and D. Reiser. CRC Press, Boca Raton, Fla. pp. 133–160.

Thurstan, R.H., McClenachan, L., Crowder, L.B., Drew, J.A., Kittinger, J.N., Levin, P.S., et al. 2015. Filling historical data gaps to foster solutions in marine conservation. Ocean Coast. Manage. **115**: 31–40. doi:10.1016/j.ocecoaman.2015.04.019.

Tiffan, K.F., Erhardt, J.M., and St. John, S.J. 2014. Prey availability, consumption, and quality contribute to variation in growth of subyearling Chinook salmon rearing in riverine and reservoir habitats. Trans. Am. Fish. Soc. **143**: 219–229. doi:10.1080/00028487.2013.839958.

Tuomikoski, J., McCann, J., Berggren, T., Schaller, H., Wilson, P., Haeseker, S., and DeHart, M. 2009. Comparative survival study (CSS) of PIT-tagged Spring/Summer Chinook and Summer Steelhead 2009 Annual Report. Comparative Survival Study Oversight Committee and Fish Passage Center. *Prepared for* Bonneville Power Administration, Portland, Ore.

Van Hyning, J. 1973. Factors affecting the abundance of fall Chinook salmon in the Columbia River. Research Reports of the Fish Commission of Oregon, **4**: 1–87.

Venditti, D.A., Kinzer, R., Barnett, B., Apperson, K.A., Tardy, K., Corsi, M.P., et al. 2015. Brood year 2012 synthesis report. [Online.] Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Res15-16VendittiISSBY2012%20Synthesis%20Report.pdf [accessed September 2018].

Visser, R., Dauble, D.D., and Geist, D.R. 2002. Use of aerial photography to monitor fall Chinook salmon spawning in the Columbia River. Trans. Am. Fish. Soc. **131**: 1173–1179. doi:10.1577/1548-8659(2002)131<1173:UOAPTM>2.0.CO;2.

Williams, R. 2006. Return to the river: restoring salmon to the Columbia River. Elsevier Academic Press, Boston, Mass.

Willson, M.F., and Halupka, K.C. 1995. Anadromous fish as keystone species in vertebrate communities. Conserv. Biol. **9**: 489–497. doi:10.1046/j.1523-1739.1995.09030489.x.

Wipfli, M.S., and Baxter, C.V. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries, **35**: 373–387. doi:10.1577/1548-8446-35.8.373.

Wipfli, M.S., Hudson, J.P., Chaloner, D.T., and Caouette, J.P. 1999. Influence of salmon spawner densities on stream productivity in southeast Alaska. Can. J. Fish. Aquat. Sci. **56**(9): 1600–1611. doi:10.1139/f99-087.

Zimmer, P.D. 1950. Observations in 1951 and 1952 of fall Chinook salmon spawning areas in the Snake River above Hells Canyon dam site. Report of US Fish and Wildlife Service, Region 1, Portland, Oregon.