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A Weight-of-Evidence Approach for Understanding the Recovery of Okanagan Sockeye Salmon

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Abstract

The productivity of Pacific Sockeye salmon (*Oncorhynchus nerka*) in the Columbia River has been declining over the past century. Yet, the Okanagan River Sockeye salmon population, which spawns in the Okanagan River, a Canadian tributary of the Columbia River, has seen a remarkable turnaround in abundance. Different hypotheses and lines of evidence covering multiple spatial scales have been proposed to explain this recovery; but they have never been comprehensively assessed. We adopted a weight-of-evidence approach to systematically assess the relative likelihood that each of these causal hypotheses contributed to the observed recovery. Our analysis disentangles the relative consequences of a set of environmental management actions that have been implemented to augment the Sockeye salmon freshwater productivity, while accounting for changes in freshwater and marine environmental conditions. Our list of potentially explanatory causal factors (anthropogenic and natural) included: (1) changes in escapement concurrent with improving local fish passage, (2) the implementation of fish-friendly flows in the Okanagan River, (3) initiating a hatchery restocking program, (4) potential improvements to Columbia dam operations to support higher relative survival of out-migrating juvenile fish, (5) possible shifts in survival-favorable conditions in the coastal marine environment for ocean-going life stages, and (6) broader changes to multi-stock harvest regimes in the Columbia River. Our assessment leveraged comparisons with the population dynamics of another Sockeye salmon stock in the Columbia River basin to differentiate between the impacts of management actions taken within the Okanagan watershed (our focus) from those occurring over the broader basin and marine scale. The results suggest that while shifts towards survival-favorable conditions in the coastal marine environment in 2007 played an important role in the upturn of the Okanagan population, alone it cannot explain the rate at which the Okanagan River Sockeye salmon recovered. Strong evidence supports the combined effect of increased escapement in conjunction with establishing and securing fish-friendly flows during spawning, incubation, and alevin emergence. Additionally, Sockeye salmon restocking improved the resilience of the stock against density-independent mortality events. These combined basin-level management actions played a pivotal role in magnifying the recovery trajectory afforded by improved marine survivorship. The spectacular response of the Okanagan River Sockeye salmon to the holistic perspectives and management interventions of Indigenous and other caretakers provides hope that other Pacific salmon stocks can be stabilized and recovered.

Keywords Okanagan River · Sockeye · Ecological flow management · FWMT · Weight of Evidence · Adaptive Co-Management

Introduction

Sockeye salmon (*Oncorhynchus nerka*|*sćwin*) that spawn in the *sq̓awsitkʷ* | Okanagan[1] River| (s|OR) along with those that spawn in the tributaries of Lake Wenatchee (Washington, United States) comprise the last two self-sustaining populations of anadromous *Oncorhynchus nerka*| *sćwin* among the eight distinct populations that formerly inhabited the Columbia River Basin (Murauskas et al. 2021). A third distinct population that spawns in the Sawtooth Valley and rears in Redfish Lake in the Snake River Basin (Idaho, Unites States) is endangered (ESA, 16 USC §1531) and maintained through hatchery production and a captive broodstock program. Pre-western contact, Indigenous Nations in the Columbia sustainably managed the

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Sockeye salmon populations (Earth Economics 2021), with peak returns ranging between 2.5 and 3.2 million fish (Chapman 1986; Fryer 1995).

Over the past 70+ years, the Sockeye salmon of the Columbia River had extensive population reductions due to anthropogenic pressures including hydroelectric dam construction and operations (habitat blockage and destruction), irrigation diversions, sawmills, other flood reduction measures, intense over fishing, mining, logging, non-native species introductions, urbanization, and agricultural floodplain development, and climate change (Nehlsen et al. 1991; Slaney et al. 1996; Hyatt and Rankin 1999; Quinn 2018). Many of these anthropogenic interventions were driven by a desire to control water resources, with little regard to fishery protection and the preservation of indigenous cultures (Ernst 1999). Since the mid-2000s provincial and federal water authorities began heeding the concerns that First Nations and American Indian Tribes have cautioned against for decades (Karilyn Alex, personal communication, March 5, 2024).

Several initiatives and programs were established in the United States and Canada to reverse the decline of Salmon populations in the Columbia River (e.g., Volkman 1996; Williams 2008; Swanson 2019). These initiatives identified four core areas for recovery: (1) improving salmon habitat (including flows), (2) setting harvest limits, (3) introducing hydropower facility (flow/passage) improvements, and (4) implementing hatchery reforms. *Billions* of dollars have been spent implementing these efforts (Jaeger and Scheuerell 2023; Northwest Power and Conservation Council 2023). Yet, the three remaining Sockeye salmon populations have responded differently over the past 20 years to these recovery actions, with the Redfish Lake population continuing at near extinction, the Wenatchee stock experiencing a modest increase, and the sǀOR Sockeye salmon returns increasing by over 400% (Fig. 1).

This has raised obvious questions about why these three populations have had very different recovery pathways and to what extent management actions contributed to their recovery. In this paper, we examine the temporal similarities and differences in the recovery trajectory of these three stocks to determine the unique factors that contributed to the recovery of the sǀOR Sockeye salmon. Comparing different stocks provides contrast and helps draw inferences about the possible drivers of the observed recovery (Marmorek et al. 2011).

The success of the sǀOR Sockeye salmon recovery has been credited to several factors that operate at different spatio-temporal scales. One set of hypotheses attributes the recovery to freshwater within-basin management actions, including: (1) increased escapement while providing improved fish passage, (2) the development and implementation of the Fish/Water Management Tool (FWMT) program in 2003–2004 (Hyatt et al. 2015) that improved fish-friendly flow conditions, and (3) the initiation of a conservation-based hatchery program in 2003. Other hypotheses attribute the recovery to out-of-basin factors that include: (1) improvements to downstream juvenile fish-passage, (2) shifts in the coastal marine environment, and (3) the listing of the Redfish Lake Sockeye salmon under the US ESA in 1991, which reduced multi-stock harvest in the lower Columbia Basin. Understanding the "*why*" will help safeguard the recovery of the sǀOR Sockeye salmon, which is critical for the *Syilx* Okanagan Nation and their relatives in the United States that have ceremonial, subsistence, and economic fisheries on the Columbia River.

In this paper, we employ a weight-of-evidence (WOE) approach to systematically disentangle and assess the credibility of different causal hypotheses (anthropogenic and natural) contributing to this unique reversal of fortune. The WOE approach has been successfully used to quantify the *relative* influence of different factors on fish productivity (Burkhardt-Holm and Scheurer 2007; Marmorek et al. 2011; Healey 2011). It is our hope that the inferences gained from this work will provide useful information to inform ongoing restoration and recovery efforts in the Okanagan Basin as well as guidance for future conservation and environmental management efforts geared towards recovering Sockeye salmon stocks in the broader Pacific Northwest. Our work also highlights remaining knowledge gaps and uncertainties in the available data that limit our ability to precisely quantify the incremental contributions made by other hypothesized factors. Recommendations are proposed to address these deficiencies.

Methodology

Study Area

Okanagan basin

The sǀOR is one of the major tributaries of the Columbia River (Fig. 2). The basin extends between the province of British Columbia (BC) in Canada and Washington State in the US. It is part of the traditional and unceded territory of the *Syilx* Okanagan Nation. Construction of dams between the 1900s and 1958 rendered most of the upper Okanagan River basin inaccessible to Sockeye salmon. Access to Okanagan and Skaha Lakes were blocked by dams in 1915 and 1921, respectively (Gustafson et al. 1997). As a result, spawning was restricted to a 20 km stretch of the river between Osoyoos and Vaseux lakes (Murauskas et al. 2021), while rearing was limited to Osoyoos Lake (Fig. 2).

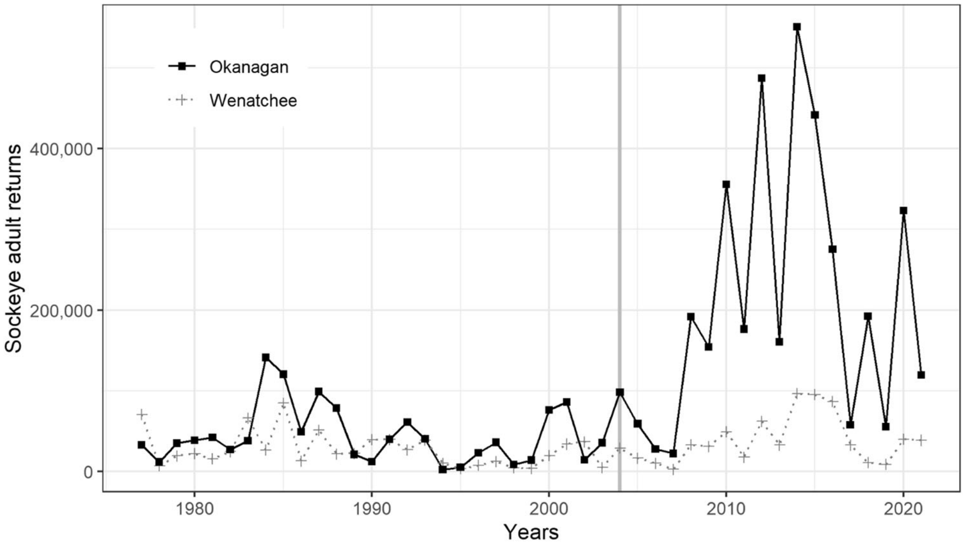

Fig. 1 Sockeye salmon returns to the mouth of the Columbia River by population (stock). Gray vertical line signifies the year (2004) when the Fish/Water Management Tool (FWMT) was fully implemented

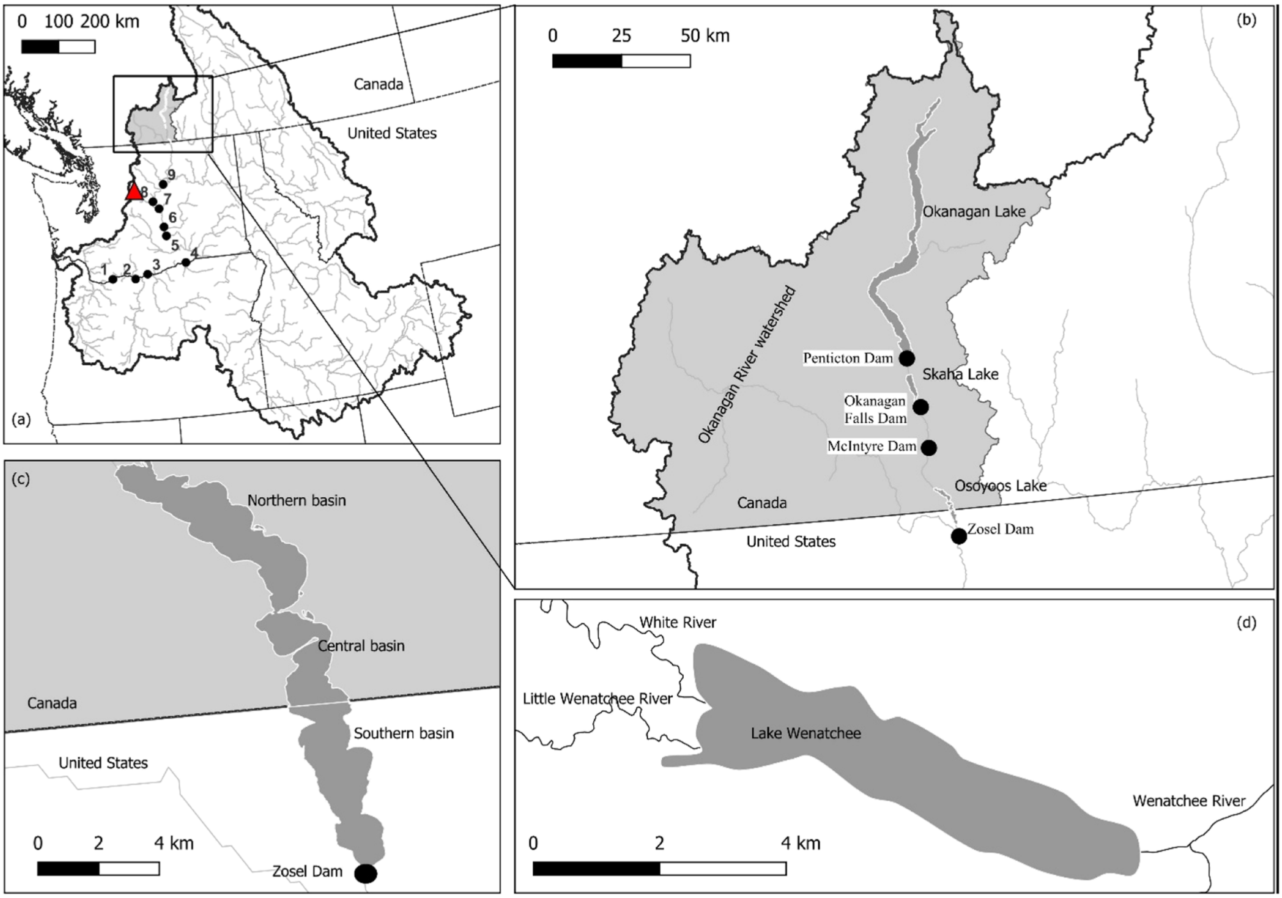

Fig. 2 **a** The Columbia River basin. Red triangle represents the location of Wenatchee Lake within the basin. Dams on the main channel of the Columbia that the s|OR Sockeye salmon have to traverse are numbered (1: Bonneville, 2: The Dalles, 3: John Day, 4: McNary, 5: Priest Rapids, 6: Wanapum, 7: Rock Island, 8: Rocky Reach, 9: Wells); (**b**) the *sq̓awsitk*^{w} | Okanagan River basin; (**c**) Osoyoos Lake; (**d**) Lake Wenatchee

Efforts by the Okanagan Nation Alliance (ONA) since 2003 have successfully reintroduced hatchery Sockeye salmon to Skaha Lake. These hatchery releases along with the reengineering of McIntyre Dam in 2009 made it considerably more efficient for Sockeye salmon to migrate to and spawn in Skaha Lake (Fig. 2). For our purposes, the term s|OR Sockeye salmon in this paper is used to include both the Osoyoos and Skaha sub-stocks.

Osoyoos Lake is mesotrophic and is divided into three basins, the northern, central, and southern basins (Simmatis et al. 2018). Its has a surface area of 9.33 km^2 and a volume of 0.278 km^3 (Hyatt et al. 2018a; McQueen et al. 2024). The shallowness of the central and south basins (max depth < 30 m) renders both unsuitable for Sockeye salmon fry/parr. This restricts age-0 Sockeye salmon to the deeper (max depth ~ 60 m) northern lake basin (Fig. 2). Water temperatures in the epilimnion often exceed 17 °C between June and September. Meanwhile in most years, dissolved oxygen (DO) levels in the hypolimnion drop below the 4 mg/L level between September and November. This restricts fry rearing habitat in the northern basin to a very narrow metalimnion that is "squeezed" between the hypoxic deep water and an overly warm epilimnion (Hyatt and Stockwell 2010). The main physico-chemical and biological characteristics of Osoyoos Lake are summarized in the Supplementary Material (Table SM1). Skaha Lake is located 50 km north of Osoyoos Lake. It has a surface area of 19.45 km^2, a volume of 0.51 km^3, and a mean depth of 26 m (Hyatt et al. 2021).

Like other Sockeye salmon, the s|OR stock has a complex life cycle. Adults return to the Columbia River in early June and commence a 1 month 986 km long journey up-river to their spawning grounds passing 10 dams to reach Osoyoos Lake (Hyatt et al. 2020) (Fig. 2). The Skaha sub-stock has one additional dam to pass. Spawning typically occurs in October. Fry then emerge between April and early May, with peak emergence happening late in April. Most fry spend 1 year rearing before smoltification and the start of their out-migration down the Columbia River towards the Pacific Ocean the following April and May. The s|OR Sockeye salmon then spend between 1 and 3 years in the ocean before returning to the Columbia River (Hyatt et al. 2018a; Murauskas et al. 2021). Sockeye salmon data sources used in this study are summarized in Table SM2.

In recent years, the s|OR stock experienced two density-independent events that negatively affected recruitment. In 2009, the Testalinden Dam failure released >200,000 m^3 of sediment and agrochemicals into the Okanagan River (Tannant and Skermer 2013). That impacted the structure of the pelagic zooplankton community and negatively impacted the abundance of juvenile Sockeye salmon for at least one to two of the following years. Additionally, in 2015, only 10% of the returning adults reached the spawning grounds due to record high water temperatures (Hyatt et al. 2020).

Wenatchee basin

The Wenatchee Sockeye (WS) salmon shares a large part of its life history with the s|OR stock. Between July and August, the WS returning adults traverse 7 dams on the Columbia River mainstem and two on the Wenatchee River on their way to Lake Wenatchee. The adults then migrate through the lake and spawn in the Little Wenatchee River (~9% average), White River (~90% average), and the Napeequa River (~1% average) (Hillman et al. 2022). After hatching, the juveniles rear in Lake Wenatchee for 1 year. Lake Wenatchee is a high-mountain oligotrophic (Fryer et al. 2020) lake that is minimally impacted by anthropogenic activities (Matala et al. 2019). Flows into the lake are almost twice as high as those entering Osoyoos Lake; yet the two lakes have similar water-particle residence time (0.7 year). While the two lakes have similar areas, Lake Wenatchee is deeper and larger than Osoyoos Lake (refer to Table SM1 in the Supplementary Material).

Given the minimal anthropogenic pressures on the Lake Wenatchee, no basin-scale interventions have been implemented on the lake or its tributaries, except for a hatchery program. Lake Wenatchee has a long history of hatchery supplementation. Beginning in 1939, Sockeye salmon broodstock originating from the Wenatchee, Okanagan, and Upper Columbia rivers were collected at Rock Island Dam and used to source a hatchery population. Approximately 58.9 million juveniles were produced and released into the lake between 1941 and 1969. After a hiatus in hatchery production, Chelan County Public Utility District resumed the release of ~200,000 juveniles annually beginning with the 1989 brood year. Assessments later found no net positive effect of the trajectory of wild Sockeye salmon recruitment or contribution to recreational harvest from hatchery supplementation. This resulted in the termination of hatchery releases following the 2011 brood year (Hillman et al. 2022).

The Wenatchee and s|OR Sockeye salmon have an overlapping marine life stage (Beacham et al. 2014), along with a partial overlap in their freshwater life stages. Differences occur during the freshwater migration (smolt downstream migration; adult upstream migration), during which the s|OR Sockeye salmon have a longer (~350 km) freshwater migration route, must traverse two additional Columbia River dams, and face more challenging temperatures along the Okanagan River. High temperatures in the lower Okanogan River can delay the arrival of returning s|OR adults by up to 3 weeks as compared to the returning WS adults (Gustafson et al. 1997; Stockwell and Hyatt 2003). WS smolts emigrate earlier than their s|OR counterparts (Gustafson et al. 1997). The latter begin their out-migration between April and May (Murauskas et al. 2021). Differences between the two populations are also attributed to their spawning and rearing habitats. Comparing these two stocks (which share a significant overlap in their lifecycle and are the only surviving self-sustaining populations of Sockeye in the Columbia River basin) is desirable as it allows for differentiating between local and broader scale

Table 1 FWMT defined "fish friendly" flows by Sockeye salmon life stage (Alexander et al. 2018)

Sockeye salmon life stage	*Main hydrology related stressor*	*Time period*	*Fish-friendly flows*
Adult migration	Poor flows during adult migration may increase bioenergetic stress and/or reduce the probability of optimal egg-deposition	August 1–31 September 1–15	10.5–28.3 m^3/s 9.1–28.3 m^3/s
Spawning	Scouring of properly sized pebbles needed for redd formation	September 16–October 31	9.9–15.6 m^3/s
Incubation	Dewatering eggs + scouring of alevins	November 1–February 15	5.0–28.3 m^3/s
Fry emergence	Dewatering eggs + scouring of alevins	February 16–April 30	5.0–28.3 m^3/s
Fry rearing	Low dissolved oxygen levels in Osoyoos lake in lake summer	Month of August or September (or both)	Average flow to Osoyoos Lake ≥10 m^3/s

factors. Note that comparison with Sockeye salmon populations outside the Columbia Basin would be confounded by a myriad of differences in habitat and ecological interactions and thus would not be appropriate choices for reference population comparisons in this analysis. Columbia River salmon, including Sockeye salmon, also experience unique habitat conditions and pressures in regard to passing multiple hydropower dams that are unique to these populations.

The Fish/Water Management Tool (FWMT)

Construction of the Okanagan water regulation system, including its main feature, Penticton Dam, at the southern most end of Okanagan Lake near Penticton, was completed in 1958 (Fig. 2). The system was completed without consultation with the *Syilx* Okanagan Nation, who foresaw its negative impacts on local Salmon habitat (Ernst 1999). Numerous memoranda of agreement between Canada and British Columbia were struck beginning in the 1950s, culminating in the 1976 Canada–BC Okanagan Basin Implementation Agreement (OBIA). Specific components of the OBIA did include the promise that "water requirements for Sockeye salmon in the Okanagan River will be met in all years except consecutive drought years". Yet, an audit of water-management performance between 1982 and 1997 identified that releases from Penticton Dam failed to meet the agreed-upon flow ranges for Sockeye salmon in 13 years of adult migration, 7 years of spawning, and 7 years of egg incubation and fry migration (Bull 1999). The results of the audit were the main motivation for the development of the FWMT.

The FWMT was designed as a multi-user internet accessible decision support tool (www.ok.fwmt.net) to improve the ability of front-line resource managers to balance multiple objectives specified by the Canada–BC OBIA as well as several additional objectives (Hyatt et al. 2015). It aims to provide predictions on the consequences of different Penticton Dam release decisions on lake elevations and river flows, fish in the Okanagan River basin, and other selected water objectives (e.g., water intakes, river recreation) (refer to Alexander et al. 2018). The tool was designed, built, tested, and calibrated between 1999 and 2003 and went into operation in water-year (and Sockeye brood year) 2004. Throughout this paper we refer to the period prior to 1999 as pre-FWMT and the period starting with 2004, as post-FWMT. The FWMT has become the primary tool for identifying in real-time water-management actions for achieving more "fish-friendly" flows and lake levels, while simultaneously guarding against flooding (Table 1).

The possible benefits of the FWMT on the s|OR Sockeye salmon stock include: (1) stabilizing flows during fall spawning, (2) predicting peak Sockeye salmon emergence time and thus the time when desiccation/scour of incubating eggs is no longer a concern, (3) highlighting potential magnitudes of egg dewatering during incubation, (3) avoiding flows that could scour alevins from redds before spring emergence, and (4) highlighting flow conditions that may offset reduced habitat rearing volumes in Osoyoos Lake. More information on the FWMT can be found in the Supplementary Material and in several published papers and reports (e.g., Hyatt and Alexander 2005; Alexander et al. 2008, 2018; Hyatt et al. 2015).

Hypothesis/Causal Explanations

Seven hypotheses/causal explanations have been proposed to explain the recovery of the s|OR Sockeye salmon population. We divided these hypotheses (contributing causal explanation) into two groups: the within-basin and the out-of-basin hypotheses/causal explanations (BH versus OH). Figure 3 summarizes the Sockeye salmon life history and identifies the life stage(s) most affected by each proposed hypothesis. Note that in presenting these hypotheses, we explore the potential for multiple contributions rather than a single cause/explanation.

Within-Basin scale hypotheses/contributing causal explanations

Within-basin hypotheses (contributing causal explanations) are unique to the freshwater habitat within the Okanagan

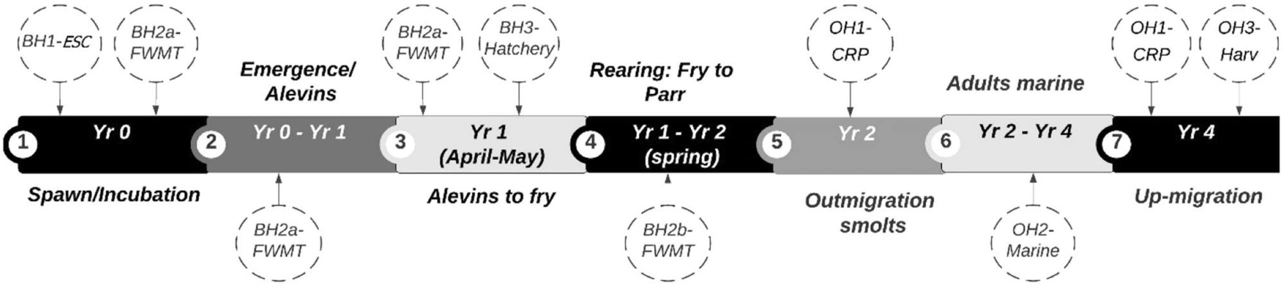

Fig. 3 Simplified life cycle of the s|OR Sockeye salmon with the potential influence of the different hypotheses. (BH1-ESC: within-basin hypothesis- changes in escapement and passage; BH2a-FWMT: within-basin hypothesis- FWMT “fish-friendly” flows; BH2b-FWMT: within-basin hypothesis- FWMT improved rearing water quality; BH3-Hatch: within-basin hypothesis- Hatchery supplementation; OH1-CRP: Out-of-basin hypothesis- Columbia River Passage; OH2-Marine: Out-of-basin hypothesis- survival-favorable conditions in the coastal marine environment; OH3-Harv: Out-of-basin hypothesis- reduced harvest rates in lower Columbia)

River basin in BC and their impacts should only be observed for the s|OR Sockeye salmon stock. Four (4) within-basin contributing causal explanations were considered in this paper:

- Hypothesis/Causal explanation BH1-ESC↑: Increased escapement targets combined with fish passage improvements propelled the s|OR Sockeye salmon population to rebound. Increased escapement also coincided with improved fish passage and habitat restoration.
- Hypothesis/Causal explanation BH2a-FWMT: Deployment and implementation of the FWMT decision-support system (Hyatt et al. 2015) in 2004 increased “fish friendly” water storage and release, which substantially reduced density-independent losses of incubating Sockeye salmon eggs and emerging fry to high flow (flood)-scour and low flow (drought)-desiccation events.
- Hypothesis/Causal explanation BH2b-FWMT: Application of the FWMT provided opportunities for higher mid-summer to early fall pulse flows from Penticton Dam that have positively affected the rearing environment in Osoyoos Lake by increasing the habitable volume of water for rearing fry. These releases improved water column turbulence and mixing and expanded the habitable space constrained by hypoxia in the hypolimnion and highly unfavorable high-water temperatures in the epilimnion.
- Hypothesis/Causal explanation BH3-Hatchery: Initiating supplemental production and release of Sockeye salmon fry into Skaha Lake substantially bolstered the rebound of the s|OR Sockeye salmon population. Releases into Skaha coincided with the re-engineering of the McIntyre Dam that allowed fish passage into the lake.

Out-of-basin hypotheses/contributing causal explanations

Out-of-basin hypotheses are associated with factors that are not under the control of Canadian entities. Their impacts are also experienced by the other Columbia River Sockeye salmon populations. The three (3) out-of-basin contributing causal explanations considered in this paper are:

- Hypothesis/Causal explanation OH1-CRP: Changes to the Columbia River dam operations improved downstream juvenile fish-passage. This supported a higher relative survival for the out-migrating juvenile fish and substantially helped the s|OR and other Columbia Sockeye salmon populations to rebound.
- Hypothesis/Causal explanation OH2-Marine: Shifts in favorable conditions in the coastal marine environment for ocean-going life stages of southern Sockeye salmon stocks resulted in substantially larger numbers of returning s|OR Sockeye salmon and other populations.
- Hypothesis/Causal explanation OH3-↓Harv: The listing of the Redfish Lake Sockeye salmon under the US Endangered Species Act (ESA) in 1991 reduced multi-stock harvest in the lower Columbia Basin thus increasing the frequency of meeting the escapement goals for the three Sockeye salmon populations in the Columbia River.

Weight-of-Evidence Approach

A range of management actions and shifts in the natural environmental conditions have occurred in the s|OR sub-basin, Columbia River, and Pacific Ocean since 1967. While potentially all these actions could affect s|OR Sockeye salmon recovery, quantitatively estimating the *precise* magnitude of each is difficult/impossible with the available data. Thus, we adopt the WOE approach to retroactively examine the body of evidence presented in terms by pathways of effect, while assessing their relative influence on causality. The WOE approach provides a systematic, logical, and transparent inferential approach to conduct a retrospective assessment of causation. It attempts to identify likely causal agents that may explain changes in ecological targets (Forbes and Calow 2002) and effectively synthesize and evaluate different lines of evidence (Forbes and Calow 2002; Burkhardt-Holm and Scheurer 2007; Marmorek et al. 2011). Suter et al. (2017) recommended assessing the relevance, explanatory strength, and reliability of each contributing causal explanation, while transparently accounting for their uncertainties and potential for bias. The WOE approach has been successfully used elsewhere to synthesize evidence to determine factors that most likely contributed to declines in Fraser Sockeye salmon (Marmorek et al. 2011; Healey 2011) and brown trout in Swiss rivers (Burkhardt-Holm and Scheurer 2007). It was also used to assess the contribution of overfishing in the Gulf of California and the Mediterranean Sea (Cánovas-Molina et al. 2021) and to understand the impacts of pink salmon on North Pacific ecosystems (Ruggerone et al. 2023).

The WOE methodology is part of the Retrospective Ecological Risk Assessment framework (Forbes and Calow 2002; Burkhardt-Holm and Scheurer 2007). Each proposed hypothesis (contributing causal explanation) is systematically analyzed with regards to a set of questions developed by Burkhardt-Holm and Scheurer (2007). This initial set of questions was adapted to meet the specificities of this study and to account for the different life-stages of the s|OR Sockeye salmon. Similar adaptations were employed by Marmorek et al. (2011), when assessing the potential factors leading to the decline of Fraser River Sockeye salmon. Our adopted WOE approach (Fig. 4) is summarized by the following:

1. Relevance: Assessed in terms of:
    a. Logical plausibility: The existence of a logically consistent mechanism between the hypothesized factor and the response variable: Does the causal relationship proposed by the hypothesis make sense logically and scientifically, and if so for which life stage of the s|OR Sockeye salmon?
    b. Exposure: Is there evidence that the s|OR Sockeye salmon population was exposed to the causal factor in question and at what life stage and for how long?
2. Explanatory strength: The strength is a property of the evidence obtained from studies/analyses. It should not be confused with the reliability of the study design or its methods (Suter et al. 2017): Is there evidence for an association between the effects seen in the s|OR Sockeye salmon population and the causal factor, either in time and/or space? Can these associations be quantified? How strong are these associations and can they be differentiated?
3. Reliability: Assessed in terms of two components:
    a. Trustworthiness of the evidence in terms of data quality (e.g., bias, experimental design, confounding factors, consistency, etc.) and quantity (Suter et al. 2017). What is the level of trustworthiness of the collected evidence? Are the available data sufficient to make conclusions?
    b. Presence of evidence from other studies to corroborate the findings: Has similar evidence been presented in comparable systems and/or for other Sockeye salmon stocks?

Using available data, we answer the above questions and assign scores that quantify the *relative* importance of each hypothesis/contributing causal factor, while indicating the affected life stage. Relative scores were assigned for relevance, explanatory strength, and reliability. Scoring within the WOE framework reduces ambiguity, clarifies the importance of the observed results, and ensures that different types of evidence will not equally influence inference (Suter et al. 2017). Scores ranged between - - - (very unlikely) and + + + (very likely). A - - - score was assigned to hypothesis/contributing causal factors that were irrelevant and/or when the collected evidence was reliable but contradicted the hypothesis. A score of + + + was assigned when the hypothesis was relevant, the collected evidence was robust, there was a strong signal in support of the hypothesis, and there was strong corroboration from other studies. A score of zero (no conclusion possible) was assigned when available data were lacking or when the collected data were relevant, had some explanatory strength, but were not supported by evidence from other relevant and trustworthy studies.

Statistical Analysis

The explanatory strength and trustworthiness for each hypothesis was determined by analyzing historic physicochemical and biological time series that reflect important life-history survival, abundance, and productivity traits of s|OR Sockeye salmon throughout their life cycle. We used the non-parametric Mann-Whitney test with unequal sample size to assess whether the median number of days with non-"fish friendly" flows in a year statistically decreased post-FWMT period for each of the life stages defined in Table 1. We also examined violations by type (i.e., violations related to low flow and violations related to high flows). Daily river flows between 1954 and 2022 at station 08NM085 Okanagan River near Oliver Station

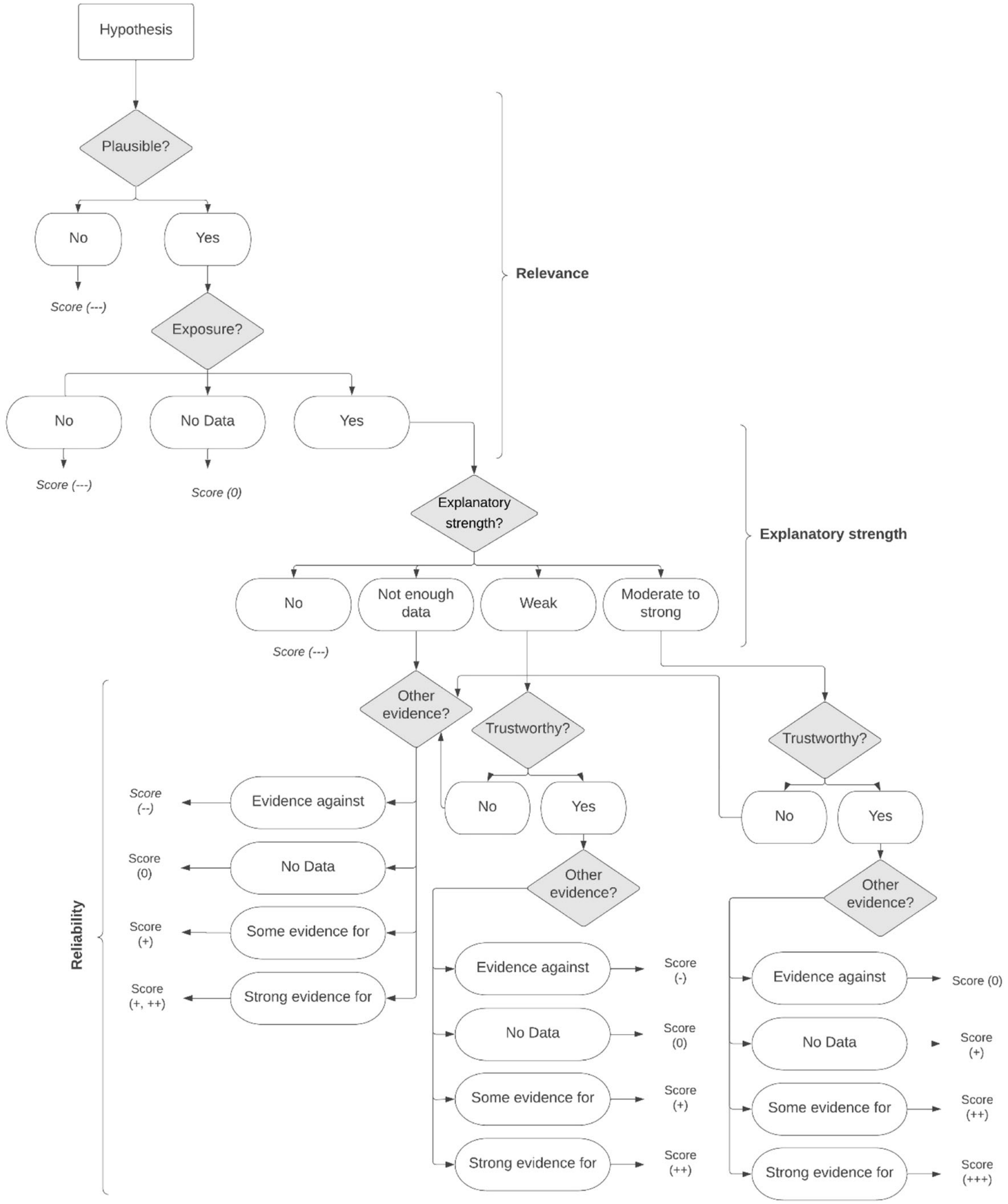

Fig. 4 The weight-of-evidence decision tree (Adapted from Marmorek et al. 2011)

were downloaded from Environment Canada (https://wateroffice.ec.gc.ca/). The Mann-Whitney test is the non-parametric equivalent of the two-sample t-test and tests for shifts in the median. When the data is not normal, the former has a higher power as compared to a t-test for a defined type-I error. For all Mann-Whitney tests we adopted an alpha value of 0.05. Analysis was conducted in the R software (R Core Team 2022). We also fit linear regression and local polynomial regression (loess) models to determine if the number of pre-smolts produced per female spawner increased post-FWMT. All models were fit in the R software (R Core Team 2022). Appropriate data transformations were implemented to ensure that the residuals of the liner regression model were normal. The 95% confidence intervals were determined and included in the generated plots.

We assessed the impacts that the FWMT had on the population of the sǀOR Sockeye salmon across its different life-stages. Annual time series data, representing different Sockeye salmon life stages, were analyzed for the presence of statistically significant changepoint(s). Capturing changepoints that correspond to basin-scale management actions is difficult given the large natural inter-annual variations in Sockeye salmon abundance, which may obscure detecting a management induced regime shift. Yet, we expect that hypotheses that are relevant and have a high explanatory strength should allow for the isolation of a signal from the background noise associated with natural environmental fluctuations. The occurrence of changepoints was assessed using the sequential t-test analysis of regime shifts (STARS) methodology (Rodionov 2004). STARS detects shifts in the mean and variance of a time series, without the typical deterioration of the test statistics towards the ends of the series (Rodionov 2005; Rodionov and Overland 2005). STARS has been successfully used to determine changepoints in environmental data, including fish and marine mammal abundance (Vert-Pre et al. 2013; Plourde et al. 2013; Gao et al. 2015). It uses a sequential data-processing technique to determine the validity of the Null hypothesis (the absence of a changepoint) at each time point. Across all analyses, a cut-off threshold, which defines the minimum length of a regime, was set to 8 years to coincide with two full generations of Sockeye salmon. A type-I error (α) of 5% was used. Further details about the implementation of the STARS analysis can be found in the Supplementary Material.

Results and Discussion

Within-Basin Hypotheses

BH1-ESC↑: Increased escapement combined with fish passage improvements propelled the s|OR Sockeye salmon population to rebound

A critical element towards restoring the s|OR Sockeye salmon population is guaranteeing that enough spawners reach suitable spawning habitat. Thus, it is plausible to assume that any increase in escapement and/or fish passage improvements will help the population rebound by allowing more spawners to lay eggs. Pre-1999 escapement varied significantly over time, ranging from as low as 1382 in 1961 up to 113,323 in 1967. Between 2004 and 2021, Osoyoos Lake spawners have averaged 57,000, with returns exceeding 100,000 in 3 years. In 1999, Hyatt and Rankin (1999) proposed defining 29,365 spawners as the *minimum* provisional escapement objective for the s|OR, while acknowledging that spawning habitat was *not* a limiting factor at that number. They recommended revising the escapement goal once the stock rebuilds, which it now substantively has (a task that at the time of writing this paper was underway by Fisheries and Oceans Canada).

Recently, O'Sullivan and Alex (2024) estimated the spawning capacity of naturally spawning Sockeye salmon in reaches above Osoyoos Lake. Their estimates were based on the Riebe et al. (2014) model that predicts spawning capacity as a function of fish length and gravel size. Their estimate, which they acknowledge is likely conservative, found that the spawning capacity above Osoyoos Lake was 137,589 Sockeye salmon (70,170 females; 67,418 males). While the O'Sullivan and Alex (2024) spawning capacity estimate may have underestimated the true spawning capacity of the system, their study provides strong evidence that the Okanagan River's spawning capacity far exceeds the ~30,000 minimum escapement goal initially recommended by Hyatt and Rankin (1999) based on the conditions and information available at that time.

For higher escapement to positively impact the s|OR Sockeye salmon population, the lake rearing environment must be able to accommodate the increased number of generated fry. Previous studies, based on observed growth and survival as well as bioenergetics modeling, reported the absence of density dependent effects on Osoyoos-rearing Sockeye salmon fry up to a density of 7000 fry ha^{-1} and an estimated carrying capacity of up to 8000 fry ha^{-1} respectively (Hyatt et al. 2019; McQueen et al. 2024). These densities can be secured with a spawning escapement goal of 150,000 returning adults (McQueen et al. 2024).

Existing evidence from Osoyoos Lake clearly shows that the spawning and rearing capacities have not yet been exceeded. Thus, the impacts of density-dependent losses (also known as "over-escapement") can be safely discounted. Moreover, ongoing efforts to restore fish passage (e.g., McIntyre Dam, Skaha Dam, Shingle Dam, Shuttleworth Creek weir removal, Ellis Creek weir removal), rehabilitate portions of the channelized river, and reintroduce Sockeye salmon to Skaha and Okanagan lakes should increase smolt production without causing density-dependent losses.

The evidence from the s|OR concurs with the conclusions made by Walters et al. (2004), who reported no evidence of a catastrophic decrease in recruitment per spawner even under high spawning stocks, when they assessed 21 British Columbia Sockeye salmon populations. A more recent study on Fraser River Sockeye salmon similarly concluded that there was no conclusive evidence to support that "over-escapement" has had a substantial negative impact on Sockeye salmon population dynamics (Peterman and Dorner 2011). These findings lead us to conclude that recent increases in escapement in conjunction with improved adult passage and stream restoration is a relevant and reliable hypothesis that has a high explanatory strength contributing to the s|OR Sockeye salmon recovery.

BH2a-FWMT: Providing “fish friendly” flows during spawning and incubation reduced losses of incubating Sockeye salmon eggs to high flow (flood)-scour and low flow (drought)-desiccation events

For Sockeye salmon, the two freshwater life stages that are most sensitive to flow disturbances are the upstream migration of returning spawners and the post-spawn egg-to-fry incubation (McDaniels et al. 2010; Healey 2011). A key objective of the FWMT was to change flow management within the s|OR to promote “fish-friendly” flows by reducing incubating egg-alevin desiccation and egg/alevin/fry scour events, with potential impacts on the rearing phase. Low flows during the egg-alevin incubation period de-water the eggs and/or alevins in the gravel, causing them to desiccate when exposed to (freezing) air temperatures (Alexander and Hyatt 2013). Meanwhile, releasing too much water during incubation creates scour, which macerates the eggs in the gravel and otherwise restricts the ability of the alevins to escape from their redds. The detrimental impacts that non “fish friendly” flows have on salmonid eggs and alevins are well documented in the literature (Schuett-Hames et al. 1996 and references within).

Before FWMT implementation, the mean number of days in a year with fish-friendly flow violations was 94 days, with significant inter-annual variability (standard deviation = 78). Post-FWMT, it dropped down to 63 days per year, with a

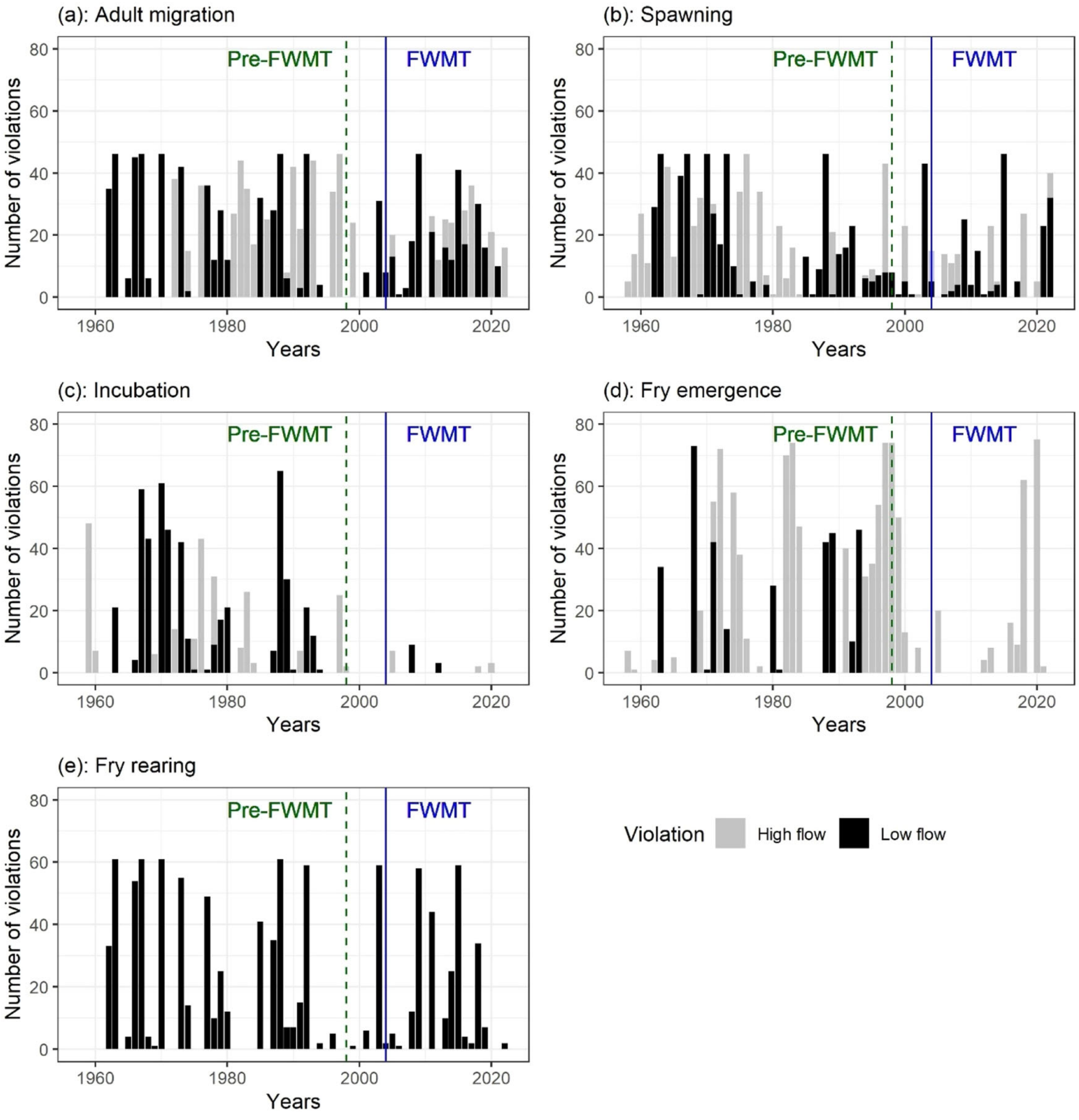

Fig. 5 Number of days each year when flows were in violation of the defined “fish friendly” flows (Table 1) by Sockeye salmon life stage. Solid blue line indicates the year when the FWMT was fully implemented in 2004. The green dashed line represents the period prior to FWMT. Period between the two lines is the period when the FWMT was being tested and calibrated. **a** adult migration stage; (**b**) spawning stage; (**c**) egg incubation stage; (**d**) fry emergence stage; (**e**) fry rearing stage

Table 2 Changes in the median occurrence of daily fish-friendly flow violations before (≤1998) and after (≥2004) the implementation of the FWMT

Life stage	Fish-friendly flow violation	*p* value[a]
Adult migration	Across all non-fish friendly violations	0.294
Spawning		0.047**
Incubation		<0.001 ***
Fry emergence		0.009 ***
Fry rearing		0.619
Adult migration	Low flow violation	0.865
Spawning		0.436
Incubation		0.002 ***
Fry emergence		0.007 ***
Fry rearing		0.619
Adult migration	High flow violations	0.569
Spawning		0.224
Incubation		0.063 *
Fry emergence		0.234
Fry rearing		NA[b]

Reported *p* values are associated with conducting a one-tailed non-parametric Mann-Whitney test (Null hypothesis: no decrease in flow violation post-FWMT; Alternative hypothesis: flow violation decreased as a result of FWMT)

[a] *** = significant at the 0.01 level; ** = significant at the 0.05 level; * = significant at the 0.1 level;

[b] NA = not applicable (lack of a high flow threshold for the rearing stage)

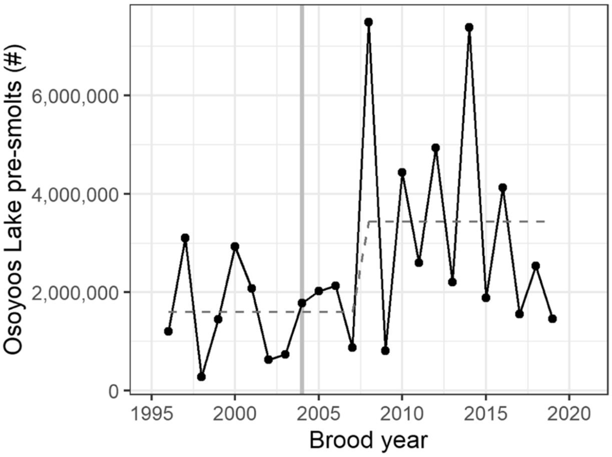

Fig. 6 Change point detection for pre-smolt abundance in Osoyoos Lake (years represent brood years). *p-value* = 0.015 for the 2007–2008 change point; changepoint detected after pre-whitening and assuming a regime length of 8 years and a Huber constant of 2 (Adapted from Alameddine et al. 2024). The gray vertical line represents the time the FWMT was implemented

standard deviation of 58. Figure 5 shows the changes in the number of flow violations over time by life stage and by type of flow violation. As can be seen, the most significant improvements occurred in the incubation and emergence life stages (Table 2). Similarly, Ng et al. (2023) found statistically significant increases in compliance rates post-FWMT for the fry incubation and fry emergence stages. A closer look at the reductions in flow violations shows that a large number of the improvements were attributed to minimizing the incidence of low flow events. Examining differences between the empirical cumulative distribution function (CDF) of river flows pre- and post-FWMT for each life stage (refer to Supplementary Material Fig. SM2) clearly shows that the probabilities of experiencing flows outside of the fish-friendly zones diminished significantly across all life stages. The greatest improvements were seen during the incubation and emergence stages. During incubation, the flow distribution was restricted within the preferred "fish-friendly" zone (Table 1). For the emergence stage, high flow violations were reduced from 24% down to 14%, while low flow violations were reduced from 11% down to 0%. This represents significant progress, particularly since high flows during the emergence stage require careful management of trade-offs between emerging fry and mitigation of flood risk (Ng et al. 2023). More modest improvements can be seen for the adult migration, spawning, and rearing life-stages, where the probabilities of flow violations remained above 20% even post-FWMT implementation.

The FWMT Sockeye salmon sub-model is also used to predict the timing of peak emergence, which is used in conjunction with field-based monitoring, to evaluate risks of water management actions to pre-emergent and migrating fry. Ng et al. (2023) assessed field-based fry peak emergence timing against those predicted by the FWMT. Overall, they found that FWMT predictions were on average 11 days early, with 44% of the annual predictions falling within the margin of error of field-based estimates of peak emergence. They concluded that FWMT predictions coupled with real-time field data have maximized the number of fry generated in a given year.

Flow improvements that reduce scour and desiccation between November and April should translate into higher egg survivorship, higher parr densities, and a higher ratio of pre-smolts to female spawners. Looking at the abundance of pre-smolts in Osoyoos Lake (Fig. 6), we see a changepoint occurring in brood year 2008 ($p = 0.015$), after which pre-smolt numbers increased by more than two-fold. The parents of the 2008 pre-smolts were the first returning adults post-FWMT implementation. Those parents benefited from the FWMT through higher survivorship during their emergence and rearing stages.

Increases in the number of pre-smolts can also be attributed to factors other than FWMT-related flow improvements. For example, out-of-basin improvements in ocean and/or Lower Columbia conditions can increase the abundance of returning adults, which in turn increase the number of eggs, fry, and pre-smolts produced in the

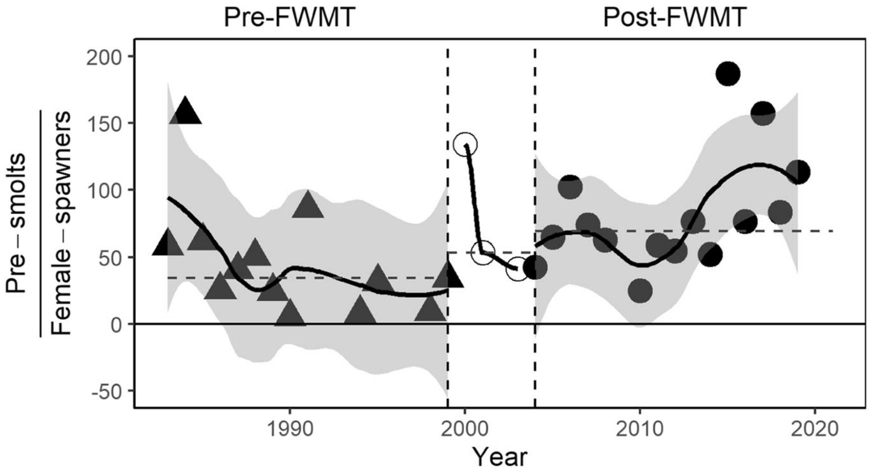

Fig. 7 Variation of the ratio of pre-smolts to female-spawners in the pre and post-FWMT period. Black solid lines represent loess lines. The 95-confidence interval is plotted in gray. Dashed horizontal lines are the median ratios for the pre-FWMT and post-FWMT periods (35 smolts per female pre-FWMT compared to 69 smolts per female post-FWMT; an increase in the median ratio of smolts per female of 97%) along with a transitional period. Data excluded the impacts of the Testalinden Dam failure and years when female-spawner numbers were estimated to be below 6000 (data excluded for 1992–1993 and 1996–1997)

freshwater life stages. To understand how much FWMT-related flow improvements increased pre-smolt survival and abundance, one needs to assess the temporal changes in the number of pre-smolts generated per natural-origin female spawner. Unfortunately, estimates of returning spawners pre-2000 are associated with high uncertainties, particularly when returns were low (Athena Ogdon, Fisheries and Oceans Canada, personal communication, December 3, 2023). As such, all years when the estimated number of returning females was below 6000 were excluded. This excluded 4 years, namely 1992–1993 and 1996–1997. We also excluded data for brood year 2009, since the failure of the Testalinden Dam decreased egg-to-fry survival (Hyatt et al. 2018a, 2018b). As can be seen from Fig. 7, the ratio of pre-smolts to female spawners generally decreased up until the early 1990s before stabilizing at a depressed rate over the next decade. The ratio recovered post-FWMT and has been increasing since. Note that the 2010 observed drop in the ratio could have been due to lasting effects from the Testalinden Dam failure in 2019 and/or to poor egg survival resulting from potential over-spawning. That year, the highest escapement of sǀOR Sockeye salmon in recent history was recorded. Spawner numbers approached the estimated spawning habitat capacity for Osoyoos Lake (O'Sullivan and Alex 2024). Field data so far have not documented evidence of redd superimposition in the system (Karilyn Alex, Okanagan Nation Alliance, personal communication, June 17, 2024.). The median ratio for the pre-FWMT period was around 35 smolts per female as compared to 69 smolts per female post-FWMT. An increase in the median ratio of smolts per female from the pre-FWMT period to the post-FWMT period of 97%.

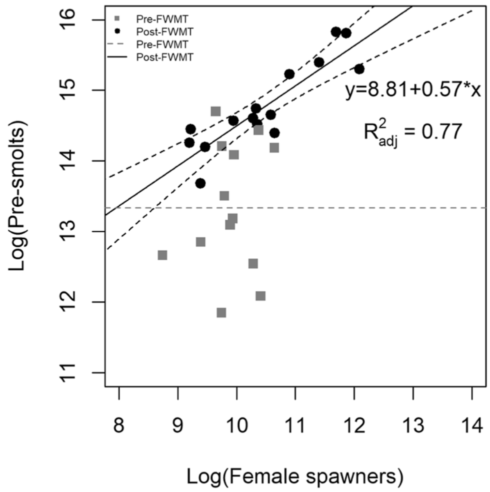

Fig. 8 Relationship between the number of Osoyoos smolts produced in a year as a function of the number of female spawners. Black solid line represents the relationship post-FWMT. Dashed black line represents the 95% confidence intervals. The gray dotted line represents the mean log pre-smolts in the pre-FWMT period. Data excluded the impacts of the Testalinden Dam failure and years when female-spawner numbers were estimated to be below 6000

Exploring the variation of Osoyoos pre-smolts as a function of the number of female spawners further (Fig. 8), we found no statistically significant correlation between the two in the pre-FWMT period. This could be a result of a heightened sensitivity to changing freshwater environmental conditions. Post-FWMT, we found a very strong relationship between the two ($R_{\mathrm{adj}}{}^2 = 0.77$; SE = 0.29). This may indicate that the impacts of environmental variability on the survival of incubating eggs (and thus variation in pre-smolt production) have been muted by FWMT-fish friendly flow operations. Smolt production is now largely a function of spawning escapement (Fig. 8). Post-FWMT, every 10% increase in the number of female-spawners resulted in an on average ~6% increase in the number of pre-smolts generated. Equally interesting is the clustering of the post-FWMT data points in the upper right quadrant, while the pre-FWMT data tended to cluster in the lower left quadrant, further highlighting the increases in both the number of spawners and pre-smolt numbers in the post-FWMT period.

Based on the evidence above, we conclude that the FWMT was a strong contributing factor for the sǀOR Sockeye salmon recovery. This conclusion was reached given the relevance of the hypothesis, the high explanatory strength associated with the collected physical evidence, the moderate explanatory strength of the available biological data, and the presence of strong supporting evidence from other studies that document how flow affects Sockeye salmon freshwater productivity.

It should be noted that another pathway by which the FWMT flows may have improved the sǀOR freshwater productivity is through increasing the spawning capacity of the system (e.g., changes in gravel quality and/or the gravel size distribution) through flow management. Yet, large sections of the sǀOR remain channelized limiting the potential to change or add new spawning habitat through flow; so, this pathway is a less plausible explanation for trends observed to date.

BH2b-FWMT: Flow mitigation improved the physical rearing environment in Osoyoos Lake by decreasing the incidence of hypoxia in the hypolimnion and lethal high-water temperatures in the epilimnion

Osoyoos Lake plays a central role in the life cycle of the sǀOR Sockeye salmon. Rearing is affected both by the productivity of the lake and the suitability of its physical environment. Both affect parr survival and their successful smoltification. During the summer, the lake suffers from low DO levels in the hypolimnion and high-water temperatures in the epilimnion. Lake temperatures exceeding 25 °C and DO levels below 2–3 ppm are lethal to rearing Sockeye salmon parr (Hyatt and Stiff 2021). While Sockeye salmon parr regularly migrate vertically in the lake to escape these lethal conditions, high temperatures (>17 °C) in the epilimnion and low DO (<4 ppm) levels in the hypolimnion may co-occur, causing juvenile Sockeye salmon to experience a ‘squeeze’ in suitable habitat that could be lethal or result in growth retardation (Hyatt et al. In Prep.).

Changes to river discharge can impact the development of the isotherm and the low DO isopleth within Osoyoos Lake’s northern basin. The FWMT river flow management protocol recommended the execution of “pulse” flow releases during September or August (or both), with sustained weekly pulses in excess of 40 m^3/s (Alexander et al. 2018). Pulse releases aimed to increase turbulent mixing. However, analyzing the water quality data collected between 1998 and 2021 showed no *sustained* pulse flows in excess of 40 m^3/s and the data did not reveal any consistent and long-term change to the habitable volume of the lake (refer to Supplementary Material; Fig. SM3).

Since the start of the FWMT program, only two high late summer pulse flows were attempted to change the physical conditions in the northern basin of Osoyoos Lake. The first occurred in September 2006, when flow releases reaching Osoyoos Lake averaged 19.23 $m^3 s^{-1}$ over 12 days. In September 2007, average flow was kept at 24.11 $m^3 s^{-1}$ for 13 days. No significant change to the physical environment of the lake was observed for both pulses (Hyatt et al. In Prep.). This may indicate that the pulse releases attempted to date were not large enough to disrupt the stratification of Osoyoos Lake. Larger releases of water in the late summer to early fall are possible but require water managers to bring Okanagan Lake levels to modestly higher than standard target elevations in late June/early July by releasing *less* water April to June and releasing the extra environmental water in *larger* ~40 m^3/s flows during portions of August—September to potentially alleviate the ‘squeeze’ in Osoyoos Lake. This requires advance forecasting of net inflows in the spring and accepting a modestly higher degree of risk taking by water managers to store more water in Okanagan Lake, a practice that must be balanced with flood protection.

McQueen and Ogden (2024) found no statistically significant relationship between the May to October average daily inflows to Osoyoos Lake and epilimnion water temperature. Yet, their analysis found a statistically significant negative correlation between river discharge on one hand and the biomass of phytoplankton. These negative correlations could be a result of reductions in water residence time (Jones 2010; Hyatt et al. 2018a) or decreased light penetration. Hence, efforts to use pulse flows to modify the habitable volume of Osoyoos lake for Sockeye salmon have the potential to temporarily reduce the productivity of the lake. Higher contrast and more sustained pulse flow experiments are required to determine potential trade-offs between reducing the oxygen-temperature squeeze and the potentially negative bioenergetic impacts on the growth of Sockeye salmon juveniles.

Based on these findings, we conclude that while this hypothesis is relevant (plausible and strong evidence of exposure), its explanatory power at the current magnitude of pulse releases is weak as there was no evidence to indicate that past implementations of small pulse flows were able to improve the physical conditions in the northern basin of Osoyoos Lake. Thus, as implemented to date, the

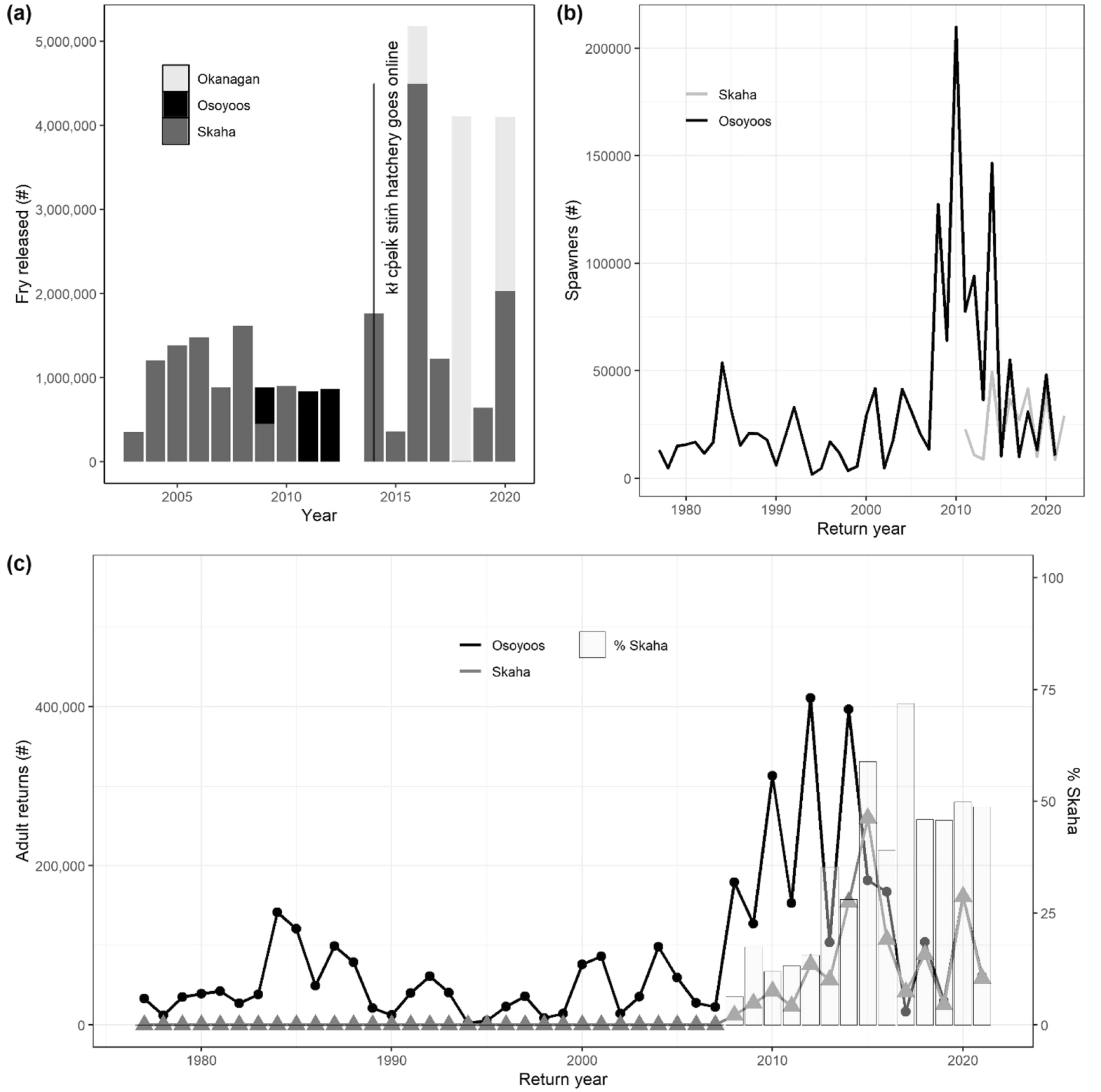

Fig. 9 **a** Stocking history in Skaha and Okanagan Lakes. Vertical line represents the year when the kł cp̓əlk̓ stim̓ hatchery went online; (**b**) spawner returns into Osoyoos and Skaha lakes by return year; (**c**) adult s|OR Sockeye salmon returns to the mouth of the Columbia River along with the percent contribution of the Skaha stock to overall annual returns

hypothesis is unlikely to explain the recovery of the s|OR Sockeye salmon.

BH3-Hatchery: Supplemental production of Sockeye salmon through the introduction of hatchery-origin Sockeye salmon fry into Skaha and Okanagan lakes

Initial attempts to reintroduce Sockeye salmon to Skaha Lake started in the summer of 2003, leveraging fry raised in Shuswap Falls hatchery. The opening of the *kł cp̓əlk̓ stim̓* hatchery in 2014 allowed the ONA to increase restocking efforts by releasing hatchery-based Sockeye salmon fry into Skaha and Okanagan Lakes. Note that both hatcheries were stocked from s|OR broodstock. As can be seen in Fig. 9a, hatchery-origin fry releases remained below 2 million up until 2016. Examining the contribution of hatchery-origin adults to the total number of s|OR-bound adult returns (Fig. 9c) to the Columbia and the numbers of spawners reaching the Okanagan basin (Fig. 9b) shows that the relative contribution of hatchery-origin Sockeye salmon significantly increased post-2015. Since then, returns have been largely equally split between the wild Osoyoos sub-stock and the hatchery-based Skaha sub-stock. These results lead us to conclude that this hypothesis is relevant. It is also very likely (strong explanatory evidence and reliability) that the restocking program contributed to the overall s|OR Sockeye salmon recovery *post-2015*. Yet, the impacts of the hatchery cannot explain the recovery of the stock prior to 2015 nor the recovery of the wild Osoyoos sub-stock. Examining changes in the population of wild Osoyoos adults over time leads us to conclude that hatchery releases supplemented a recovery trajectory that was already underway.

Out-of-Basin Hypotheses

These hypotheses operate on a regional scale and thus should affect the s|OR Sockeye salmon population as well as the other Sockeye salmon populations in the Columbia River basin (namely the Wenatchee) and/or other Sockeye salmon populations along the Pacific coastline.

OH1-CRP: Improvements in juvenile fish-passage in the Columbia River were responsible for the observed population rebound

Upon listing the Upper Columbia River spring Chinook Salmon and steelhead in the mid-1990s on the ESA, operational changes were made to the hydropower system in the Columbia River to improve passage facilities at dams and to modify flow and spill operations to improve juvenile migration and increase survivorship of both adult and juvenile salmonids. Among these changes was the institution of a court-ordered spill in 2006 to release extra water over dams for fish migration, and the installation of surface collectors at four additional dams to attract, safely holds, and provide downstream passage to juvenile salmon. These changes have decreased average travel time for smolts (Widener et al. 2018) and reduced rates of turbine mortality (Skalski et al. 2021).

In 2007, further programs were instituted at most dams to encourage juvenile spillway passage by increasing spill and using surface-passage structures. Since then, spill has become the primary management strategy to increase survival of juvenile fish passing dams within the Federal Columbia River Power System. However, the quality of evidence gathered to verify higher rates of survival resulting from spillway passage has been limited due to the low probabilities of passive integrated transponders (PIT)-tag detection as fish pass through spillways (Widener et al. 2018). Existing PIT-tag data suggests that s|OR smolts have shown a relatively high rate of survival (~87% per 100 km) during their juvenile outmigration as compared to Fraser smolts, whose survival was estimated to range between 50 and 70% per 100 km (Murauskas et al. 2021). Yet, it is not clear how much of that rate can be attributed to the improvements to fish-passageways in the Columbia.

While there is evidence of improved juvenile passage survival across the Columbia River hydroelectric projects, the Lake Wenatchee population did not exhibit a recovery of the same magnitude as the Okanagan population even though the latter has to bypass two additional dams. Thus, we conclude that the line of evidence associated with juvenile passage improvements is a relevant but weak (low explanatory strength and lack of similar responses from all affected stocks) explanation for the recovery of s|OR Sockeye salmon.

OH2-Marine: Shifts in survival-favorable conditions in the coastal marine environment for ocean-going life stages of southern Sockeye salmon stocks resulted in substantially larger numbers of returning s|OR Sockeye salmon and other populations

Beacham et al. (2014) tracked the ocean migration pathways of several Pacific juvenile Sockeye salmon stocks, including the Columbia River populations (Wenatchee, Okanagan, and Redfish). They found that the three stocks had a similar ocean migratory route. They migrated along the coast of Washington and reached the west coast of Vancouver Island by June. Individuals from these populations then migrated to the northern tip of Vancouver Island. The majority then moved into the Queen Charlotte Sound and the Hecate Strait regions. Wenatchee and s|OR Sockeye salmon were also found to migrate to areas off the west coast of Haida Gwaii and Southeast Alaska. WS were observed in the summer in the Prince William Sound region, while some s|OR Sockeye salmon were observed in Southeast Alaska during the fall. Given the similarity of the migration pathways of both stocks, it is reasonable to assume that changes in ocean conditions should similarly affect the marine survivability of all three Columbia River populations.

The abundance of salmon naturally varies, with synchronous variations amongst different stocks observed at times across wide regions. These patterns are often a result of large-scale climatic changes, such as the Pacific Decadal Oscillation (Mantua et al. 1997) and the El Niño Southern Oscillation (Fiedler and Mantua 2017). Columbia River Sockeye salmon juveniles are affected by the conditions in the northern California Current System (CCS) during their first year of marine life (Williams et al. 2014; Crozier et al. 2019). Variability in Sockeye salmon marine productivity is known to correlate with the occurrence of La Niña and El Niño anomalous ocean conditions that impact available food levels (Thomson et al. 2012; Bussanich et al. 2018).

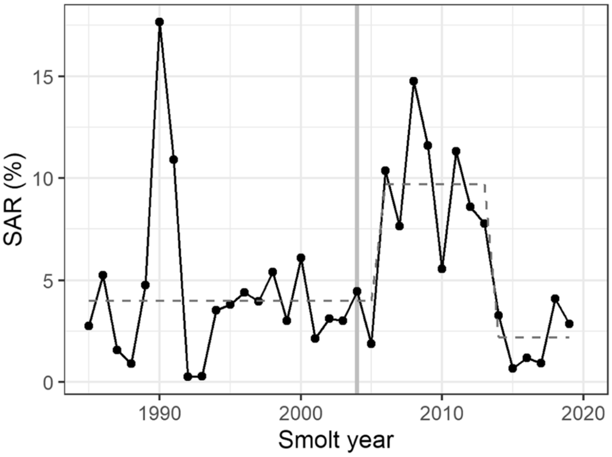

Fig. 10 Smolt to adult Returns (SAR) ratio (%) for sl|OR Sockeye salmon between smolt year 1985 and 2019. Gray-dashed line is the detected STARS regime shift over time (*p*-value for 2005–2006 change points <0.01; *p*-value for 2013-2014 change points <0.01; changepoints detected after pre-whitening and assuming a regime length of 8 years and a Huber constant of 2)

Unfortunately, it is not possible to generate a direct annual 'marine survival' value for the sl|OR and Wenatchee Sockeye salmon because of fundamental sampling limitations. One must instead infer the impacts of the marine environment on the returning stocks based on imperfect data, such as the smolt-to-adult return (SAR) ratio, which is a measure of survival that encompasses multiple freshwater and marine life stages, including smoltification, outmigration from rearing lakes, estuary/ocean residency, and the adult return phases (Williams et al. 2014). Despite this aggregation, assessing temporal changes in the annual SAR ratio still provides an index of marine survival, as the primary sources of mortality mostly occur in the marine environment, especially in the first months of marine residency (Beamish et al. 2004; Williams et al. 2014).

For the sl|OR Sockeye salmon, two temporal changepoints in the SAR time series were supported by the data (Fig. 10). The first occurred during the 2006 smolt outmigration year. SAR averaged ~4% between 1985 and 2005. It increased to ~10% as of 2006. SAR remained high until 2013, after which it dropped to an average of ~2% (2014–2019). According to NOAAs's Ocean Ecosystem Indicators (OEI) for Pacific salmon, marine survival in the Northern California Current (NCC) started to improve in 2006, and 2008 was the best year across the OEI time series for juvenile salmon entering the NCC (NOAA, 2023). The second changepoint for sl|OR SAR occurred in 2014; it coincided with adverse marine conditions as reported by the Northwest Fisheries Science Center. As a matter of fact, 2015 and 2016 were two of the worst years in terms of physical and biological ocean conditions for juvenile salmon entering the NCC since 1998, and the years 2014–2017 along with 2019 ranked in the top 10 worst years (NOAA). Increased competition between Sockeye salmon and Pink salmon in the North Pacific was linked to the decline of Sockeye salmon productivity during odd years (Ruggerone and Connors 2015; Ruggerone et al. 2023). This could explain part of the inter-annual variability in SAR, yet it is unlikely to explain the overall increase in the mean SAR post-FWMT.

Regarding the WS, data limitations do not allow for the assessment of temporal changes in SAR prior to the 2013 smolt migration year. Overall, the temporal variability in the WS SAR since 2013 corresponds with the pattern observed for the Okanagan SAR (Spearman's correlation = 0.58; $p = 0.10$). This reinforces the likelihood that changes in marine conditions were a major driver of adult Sockeye salmon population variability for both stocks. It is safe to conclude that this hypothesis is relevant, has strong explanatory power, and is reliable in contributing to the pattern of recovery of Okanagan Sockeye salmon.

OH3-↓Harv: The listing of the Redfish Lake Sockeye salmon under the US ESA in 1991 reduced harvest in the lower Columbia Basin and thus increased the frequency of meeting escapement goals for the three Sockeye salmon stocks in the Columbia River

Fishing pressure can result from marine and/or freshwater harvests. The Columbia lacks a directed marine fishery and thus the fishing pressure is a result of freshwater harvest. Harvest pressures in the Columbia River have varied significantly over time. The listing of the Redfish Lake Sockeye salmon under the ESA in 1991 led to restrictions on the harvest of Sockeye salmon in the lower Columbia. Prior to the ESA listing, harvest rates often exceeded 20% of total returns, with some years exceeding 45%. Post listing, the harvest rates were set to be below 8% of returning adults.

ESA harvest restrictions benefited the sl|OR and Wenatchee Sockeye salmon stocks, since the Redfish Lake-origin Sockeye salmon return to the lower Columbia River at the same time (Hyatt and Stockwell 2019). Nevertheless, tribal and recreational harvests above the mid-Columbia River remained stock specific and were not affected by the ESA. As can be seen from Fig. 11a, the WS experienced high harvest rates between 2004 and 2016. Meanwhile, harvest pressures for the Okanagan stock remained low between 1989 and 2009 (Fig. 11b). In 2009, harvest of sl|OR Sockeye salmon was allowed to increase from an average of 10,000 fish to an average of 69,000 fish per year (Hyatt et al. 2020). Recent harvest rates even exceeded those recorded in the late 1980s. The largest portion of the sl|OR Sockeye salmon harvest happens in the river reaches that are exclusively used by that stock and thus does not affect the WS.

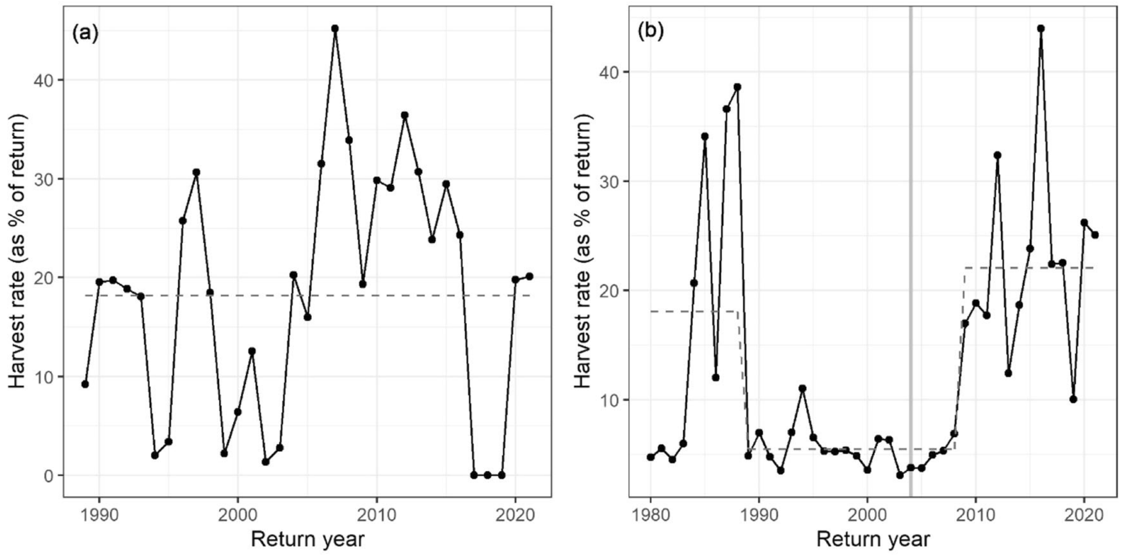

Fig. 11 Harvest rates as a percentage of adult return for (**a**) Wenatchee Sockeye salmon (including commercial (zones 1–5), recreational, and tribal harvest (above Tumwater Dam)); (**b**) s|OR Sockeye salmon (including harvest both above and below Wells Dams). Dashed gray lines represent mean harvest rates in a time period. No change-point was detected for Wenatchee Sockeye salmon harvest. Two changepoints were detected for s|OR Sockeye salmon harvest; (*p*-value for the 1988–1989 change point was 0.02; *p*-value for the 2008–2009 changepoint was <0.001). Years represent return years. Refer to Fig. 2 to locate Tumwater and Wells dams (National Marine Fisheries Service West Coast Region 2014; Judson et al. 2023; Alameddine et al. 2024)

The discrepancy in harvest pressure between the two stocks could partially explain the divergent recovery trajectories. It is well established that reductions in harvest offer a means to mitigate the risks for salmon stocks that bear substantial pre-spawn mortality pressure; but, they are unlikely to increase population growth rates enough to produce stable or increasing trends for stocks that are constrained by other factors (McClure et al. 2003). Harvest pressure up to the early 1990s contributed to the decline of all three Columbia Sockeye salmon stocks. Nevertheless, had harvest pressure been the only cause contributing to the collapse of the Columbia Sockeye salmon, then we would have expected a concurrent rebound of all three stocks post-1990. Since the Redfish stock has yet to show signs of recovery following strict harvest management and the s|OR stock recovered 14 years post ESA-enforced harvest reduction, we can conclude that while the hypothesis is relevant, its explanatory strength to explain the recovery of the s|OR Sockeye salmon population is weak. Nevertheless, the impacts of recent increases in s|OR Sockeye salmon harvest above and below Wells Dams needs to be further examined as more data becomes available.

Conclusions

The s|OR Sockeye salmon population's recovery was a result of a series of management interventions and fortunate natural events that together brought this stock back from the brink. Without *all* of these factors, the s|OR Sockeye salmon recovery would not have been as impressive. We found evidence that increased escapement, reducing harvest pressure, and improving fish passage allowed for more spawners to reach their spawning grounds, naturally generating far larger numbers of eggs. Moreover, the recovery of the s|OR Sockeye salmon is also a bright example of the effectiveness of basin-scale flow management. Promoting fish-friendly flows substantially supported the fragile early life stages of the s|OR Sockeye salmon, namely the incubation and emergence phases, thus increasing freshwater productivity. Management efforts like this that secure high freshwater productivity are important contributors to resilience and recovery. Finally, the decision of the ONA to reintroduce Sockeye salmon to Skaha Lake further helped improve the resilience of the s|OR population to density-independent mortality events and expanded their range.

The result of our analysis also highlighted the important impact that ocean conditions in the NCC system has had on the Columbia Sockeye salmon stocks. While knowledge of its impact is not new (Mueter et al. 2002; Martins et al. 2012; Cheung and Frölicher 2020; Hyatt and Stiff 2021), we were able to document the synergy between favorable marine conditions and effective within-basin management. Relying only on favorable marine conditions for recovery would have been insufficient for the s|OR Sockeye salmon population to turn the corner towards recovery in the mid-2000s. That was evident with the failure of the Wenatchee sockeye salmon to show a similar recovery trajectory during some of the most favorable ocean years in recent decades. Moreover, had the within-basin management actions not coincided with these years of favorable marine conditions, the recovery would likely have been smaller and/or delayed.

While sometimes dissatisfying, the complex life cycle and large geographic habitat domain of the s|OR Sockeye salmon along with practical constraints on the granularity of data collection obscures the precise quantification of individual drivers on the population. Effects on one life stage are known to carry forward to subsequent life stages and across generations, such that the cumulative impact is often greater than the impact on any individual life stage (Healey 2011). Additionally, Sockeye salmon experience different density-dependent and compensatory dynamics as they move through their life cycle that sometimes-offset losses/gains in prior stages. These all highlight the practical challenges resource managers face in making wise decisions for these fish. Fortunately, the availability of long-term data, the presence of closely related stocks in the Columbia River basin, as well as the restorative interventions operating at different spatio-temporal scales allowed us to examine different causal factors using a WOE approach. While we used the full breadth of evidence and data collected over more than 35 years (Table 3), we are cognizant that not every possible causal explanation and piece of evidence was captured in this synthesis and there will always be additional hypotheses that exist beyond those assessed (Table 3). For example, we did not consider hypotheses that looked at the impacts of predation or exposure to pathogens. Future work should assess if these stressors disproportionally impact one stock.

Given the uniqueness of the s|OR Sockeye salmon population, it is hard to generalize our findings to other Pacific Sockeye salmon populations that are predominantly experiencing a downturn in their abundance. However, our results showcase how basin-scale management actions can add layers of resilience towards recovering Sockeye salmon stocks, thus providing hope that other Pacific Salmon stocks can be stabilized and recovered. One may ask, does our analysis predict a sustained recovery and safe future for the s|OR Sockeye salmon? The answer to this question is determined by future survival conditions and cannot be answered through the WOE approach, an inherently retrospective form of analysis (Marmorek et al. 2011). While only the future will reveal the answer, the s|OR Sockeye salmon story illustrates the importance of sustaining restoration efforts and seeking additional management pathways that add additional layers of resilience (e.g., continuing range re-introductions into additional habitats).

This work has also highlighted the urgent need to revise the escapement goal for the s|OR Sockeye salmon given the ability of the freshwater habitat to support larger numbers of successful spawners and to ensure that increased harvest pressure does not wipe out these hard-fought management efforts. This will support bilateral discussions between Canada and the US on revising the exiting total harvest rate and harvest sharing agreement for Sockeye salmon. It is our understanding that Fisheries and Oceans Canada and Indigenous fisheries groups have initiated that process with the relevant bi-lateral management entities (Athena Ogden and Karilyn Alex, personal communication, July 19, 2024).

What is certain is that s|OR Sockeye salmon, like many Pacific Sockeye salmon, are highly vulnerable to the impacts of climate change (Marmorek et al. 2011; Healey 2011; Hyatt and Stiff 2021). While Sockeye salmon in the Columbia River have been adapting to altered river conditions, with contemporary adults migrating, on average, more than 10 days earlier than they did in the 1940s (Crozier et al. 2019), vital questions remain if these and other adaptations will be fast enough. The record high river temperatures observed in 2015 may be a prelude to what this population will be experiencing at a higher frequency in the future. There is also a risk that the contribution of Osoyoos Lake to the natural-origin Sockeye salmon population may ebb, given its sensitivity to temperature-induced habitat "squeeze". Ensuring that all Osoyoos, Skaha, and Okanagan Lakes have sustainable Sockeye salmon populations may provide the s|OR stock with a larger latitude to adapt and endure the challenges of a warming climate. While managing the impacts that climate change may have on the s|OR *marine* life stage is currently not possible, this study shows that there are opportunities to dampen the marine impacts during freshwater life-stages.

Our WOE study also allowed us to identify some of the most relevant known unknowns that will guide future monitoring efforts to better quantify the causal pathways influencing s|OR Sockeye salmon recovery. They primarily include expanding existing monitoring efforts to unpack the different factors contributing to freshwater productivity. This will require tracking inter-annual changes in fecundity, sex ratio, egg-to-fry, and fry-to-smolt survival rates. Similarly, more data are needed to better understand the annual variability in smolt out-migration (i.e., pre-smolt to smolt survival at ocean entry). There is also a need to understand the potential interplay between natural-origin and hatchery-origin sub-stocks, as the s|OR Sockeye salmon population continues to reestablish itself in Skaha and Okanagan lakes. Continuing to embrace an adaptative management approach will help managers to track competition between Sockeye salmon, kokanee, and other resident fish in Osoyoos, Skaha, and Okanagan lakes. While our analysis did not show any evidence of density-dependent declines for the s|OR Sockeye salmon, record breaking adult returns in 2010 (176,476 spawners) were suspected to have culminated in redd superimposition, which reduced egg survival (Hyatt

Table 3 Summary of the hypotheses/contributing causal factors to explain the sǀOR Sockeye salmon using the WOE approach

Hypothesis/Contributing causal explanation	*Relevance (plausible and existence of an exposure mechanism)*	*Explanatory strength*	*Reliability*	*Overall influence on causality (H/M/L)*
BH1-RES↑: Escapement goal capped potential production far below the maximum carrying capacity available for freshwater Sockeye salmon Spawning and rearing. Revising the historic escapement objective upwards combined with improved fish passage propelled sǀOR Sockeye salmon population to rebound.	+++	+++	+++	H
BH2a-FWMT: Deployment and implementation of the real-time FWMT decision-support system (Hyatt et al. 2015) post-2004 facilitated “fish friendly” water storage and release decisions that substantially reduced density-independent losses of incubating Sockeye salmon eggs and fry to high flow (flood)-scour and low flow (drought)-desiccation events and increased freshwater productivity (number of surviving pre-smolts per female spawner).	+++	++	+++	H
BH2b-FWMT: Application of FWMT post-2004 identified opportunities for higher mid-summer to early fall pulse flows from Penticton Dam positively affected the rearing environment in Osoyoos Lake by increasing the habitable volume of water for rearing Sockeye salmon fry.	+++	0	Unknown – larger pulse flow experiments needed	L
BH3-Hatchery: Initiating supplemental production and release of Sockeye salmon fry into Skaha Lake starting in 2003 substantially helped the sǀOR Sockeye salmon population to rebound.	+++	++	++	H (in later years)
OH1-CRP: Changes to Columbia River dam operations improved downstream juvenile fish-passage supporting higher relative survival of out-migrating juvenile fish and substantially helped the sǀOR Sockeye salmon population to rebound.	+++	+	0	L
OH2-Marine: Shifts in survival-favorable conditions in the coastal marine environment for ocean-going life stages of southern Sockeye salmon stocks resulted in substantially larger numbers of returning sǀOR Sockeye salmon and other populations.	+++	+++	+++	H
OH3-↓*Harv*: The listing of the Redfish Lake Sockeye salmon under the US ESA in 1991 reduced multi-stock harvest in the lower Columbia Basin and thus increased escapement for the three Sockeye salmon populations in the Columbia River, substantially helping the sǀOR Sockeye salmon population rebound.	+++	+	+	L

+++ = very likely; ++ = moderately likely; + = probably likely; 0 = no conclusion possible; - = probably not likely; -- = moderately unlikely; --- = strongly unlikely

H highly credible and very likely; *M* moderately credible evidence and likely; *L* low credibility and unlikely et al. 2018a), increase fry mortality, and reduced fry growth (McQueen et al. 2024). Thus, the population needs to be continuously monitored to document density-dependent impacts on spawning and rearing. Moreover, there is a need to expand coordination between the responsible agencies in Canada and the US to standardize the collection of data (i.e., number of redds, fecundity, date of emergence, fry and smolt abundance, smolt outmigration date, and spawner sex ratio) on the three remaining Columbia Sockeye salmon stocks. This includes additional care and attention to carefully calibrate and unify sampling methodologies for the metrics noted earlier.

Finally, it is important to recognize that the success of the FWMT program is largely attributed to the superb coordination and cooperation between the *Syilx* Okanagan Nation, Fisheries and Oceans Canada, and the BC Ministry of Environment and Climate Change Strategy throughout its more than 20-year development and implementation. It is also one of a growing number of cases that underscores the importance of embracing First Nations' knowledge, cultural, and spiritual beliefs that propel a desire to steward and co-manage resources in their traditional territories, including implementing ecological restoration actions (Broadhead and Howard 2021). Furthermore, the Okanagan program showcases the value of adopting an adaptive management framework with a long-time horizon and commitment to sustained monitoring when embarking on recovering a population. We would argue that embracing such a multi-faceted framework has never been more critical given the complexities being brought about by a changing climate.

Data Availability

The data that support the findings of this study are not openly available due to reasons of sensitivity and are available from the corresponding author upon reasonable request. Data are located in controlled access data storage at the Okanagan Nation Alliance.

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Acknowledgements This story is just the beginning of a "coming in," or coming to better understand our relationship to place and value in community, culture, history, and the larger vision of the Okanagan Nation Elders to heal the river by "bringing it back" kt cp'əlk' stim'. Indeed, this work stands on the shoulders of Okanagan Nation elders, leaders, knowledge keepers, youth, and others who have desired for over 100 years to re-establish a balanced ecosystem approach to water management for salmon. To the present-day, *Syilx* Okanagan community members have prioritized being on the land and water to measure and observe the results of FWMT (Colette Louie, Dawn Machin, Lindsey George, Casmir Tonasket, and many others). *Syilx* leadership was crucial to the establishment of the governing Canadian Okanagan Basin Technical Working Group and its related efforts to re-introduce and restore Okanagan Sockeye, including the creation of the FWMT. Funding for FWMT and this study was generously provided by Douglas County Public Utility District of Washington State. The authors are grateful to Tom Kahler and the late Rick Klinge who both steadfastly supported FWMT, including the FWMT modernization effort between 2015–2018. Enacting a *Syilx*-ethic of gratitude, relationship, and acknowledgement, several non-native scientists and resource managers added their support and expertise to the story of Okanagan salmon restoration, including Brian Symonds, Athena Ogden, Don McQueen, Howard Stiff, Margot Stockwell, Paul Rankin, Lynnea Weins and Chelsea Mathieu. And a very special acknowledgement is owed to the late Dr. Kim Hyatt ("Dr. Sockeye") who passed away May 25, 2021. Kim's devotion to work towards recovery and adaptive management of Okanagan River Sockeye as well as his special ability to unify funders, researchers, and managers were absolutely pivotal to the success of FWMT. He has etched a deep desire in many to continue being bridge builders and to uphold the optimistic view of what is possible when we give nature a chance.

Author Contributions All authors contributed equally towards the study's conception and design. KA and DM contributed to data collection and curation from federal, provincial, and First Nation agencies. CA and IA implemented the statistical analysis and model development. All authors contributed equally to the analysis and interpretation of results. CA and IA wrote the main manuscript text and produced the figures. CA and KA coordinated research activity planning and execution. All authors reviewed the results and approved the conclusion presented in the final version of the manuscript.

Compliance with Ethical Standards

Conflict of Interest The authors declare no competing interests.

References

Alameddine I, Stiff HW, Judson B, Ogden AD (2024) Comparisons of population dynamics of Sockeye salmon (Oncorhynchus nerka) in two Columbia River populations: Osoyoos Lake (British Columbia) and Lake Wenatchee (Washington State). Fisheries and Oceans Canada Science Branch, Pacific Region Salmon in Regional Ecosystems Program, Pacific Biological Station, Nanaimo, BC

Alexander CAD, Hyatt KD (2013) The Okanagan fish-and-water management tool (Ok-FWMT) record of design (v. 2.4.000). Canadian Okanagan Basin Technical Working Group

(COBTWG) and Douglas County Public Utility District No. 1 (DCPUD), Kamloops, BC

Alexander CAD, Hyatt KD, Symonds B (2018) The Okanagan Fish/Water Management Tool: guidelines for Apprentice Water Managers-v.3.0 (post 2015-2018 Modernization). Canadian Okanagan Basin Technical Working Group, Kamloops, BC

Alexander CAD, Hyatt KD, Symonds B (2008) The Okanagan fish/water management tool: guidelines for apprentice water managers (v.2.1.000). Canadian Okanagan Basin Technical Working Group and Douglas County Public Utility District, Kamloops, BC

Beacham TD, Beamish RJ, Candy JR et al. (2014) Stock-specific migration pathways of juvenile Sockeye salmon in British Columbia waters and in the Gulf of Alaska. Trans Am Fish Soc 143:1386–1403. https://doi.org/10.1080/00028487.2014.935476

Beamish RJ, Mahnken C, Neville C (2004) Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. Trans Am Fish Soc 133:26–33

Broadhead L-A, Howard S (2021) Confronting the contradictions between Western and Indigenous science: a critical perspective on Two-Eyed Seeing. AlterNative Int J Indig Peoples 17:111–119. https://doi.org/10.1177/1177180121996326

Bull CJ (1999) Fisheries habitat in the Okanagan River phase 2: investigation of selected options. Public Utility District of Douglas County, WA, East Wenatchee, WA

Burkhardt-Holm P, Scheurer K (2007) Application of the weight-of-evidence approach to assess the decline of brown trout (Salmo trutta) in Swiss rivers. Aquat Sci 69:51–70. https://doi.org/10.1007/s00027-006-0841-6

Bussanich R, Hyatt KD, Wright H (2018) Proceedings of an Expert's Workshop on Columbia River and Hydro-system Impacts on Migration Success and Production Variations of Anadromous Salmon, Dec. 6–7, Portland Oregon

Cánovas-Molina A, García-Charton JA, García-Frapolli E (2021) Assessing the contribution to overfishing of small- and large-scale fisheries in two marine regions as determined by the weight of evidence approach. Ocean Coast Manag 213:105911. https://doi.org/10.1016/j.ocecoaman.2021.105911

Chapman DW (1986) Salmon and steelhead abundance in the Columbia River in the nineteenth century. Trans Am Fish Soc 115:662–670

Cheung WW, Frölicher TL (2020) Marine heatwaves exacerbate climate change impacts for fisheries in the northeast Pacific. Sci Rep. 10:1–10

Crozier LG, McClure MM, Beechie T et al. (2019) Climate vulnerability assessment for Pacific salmon and steelhead in the California Current Large Marine Ecosystem. PLoS ONE 14:e0217711

Earth Economics (2021) The sociocultural significance of Pacific salmon to tribes and first nations. Special Report to the Pacific Salmon Commission, Tacoma, WA

Ernst A (1999) Okanagan Nation Fisheries Commission Dam Research: Final Draft. Okanagan Nation Fisheries Commission, Westbank, BC

Fiedler PC, Mantua NJ (2017) How are warm and cool years in the California current related to ENSO? J Geophys Res Oceans 122:5936–5951

Forbes VE, Calow P (2002) Applying weight-of-evidence in retrospective ecological risk assessment when quantitative data are limited. Hum Ecol Risk Assess 8:1625–1639. https://doi.org/10.1080/20028091057529

Fryer JK (1995) Columbia Basin Sockeye salmon: causes of their past decline, factors contributing to their present low abundance, and future outlook. University of Washington

Fryer JK, Kelsey D, Wright H et al. (2020) Studies into factors limiting the abundance of Okanagan and Wenatchee Sockeye salmon in 2018. Columbia River Inter-Tribal Fish Commission, Portland, OR

Gao J, Holden J, Kirkby M (2015) A distributed TOPMODEL for modelling impacts of land-cover change on river flow in upland peatland catchments. Hydrol Process 29:2867–2879

Gustafson RG, Wainwright TC, Winans GA et al. (1997) Status review of Sockeye salmon from Washington and Oregon. United States Department of Commerce, National Oceanic and Atmospheric Administration, Seattle, WA

Healey M (2011) The cumulative impacts of climate change on Fraser River Sockeye salmon (Oncorhynchus nerka) and implications for management. Can J Fish Aquat Sci 68:718–737. https://doi.org/10.1139/f2011-010

Hillman T, Miller M, Shelby K, et al (2022) Monitoring and evaluation of the Chelan and Grant County PUDs hatchery programs: 2021 annual report. Wenatchee and Ephrata, WA

Hyatt KD, Alexander CAD (2005) The Okanagan fish-water management (OKFWM) tool: results of a 25-year retrospective analysis. Canadian Okanagan Basin Technical Working Group, Kamloops, BC

Hyatt KD, Alexander CAD, Stockwell MM (2015) A decision support system for improving "fish friendly" flow compliance in the regulated Okanagan Lake and river system of British Columbia. Can Water Resour J 40:87–110. https://doi.org/10.1080/07011784.2014.985510

Hyatt KD, McQueen DJ, Ogden AD (2018a) Have invasive mysids (Mysis diluviana) altered the capacity of Osoyoos Lake, British Columbia to produce Sockeye salmon (Oncorhynchus nerka)? Open Fish Sci J 11:1–26

Hyatt KD, McQueen DJ, Ogden AD et al. (2021) Age-structured interactions among reintroduced Sockeye salmon, resident Kokanee, Invasive Mysids, and their Zooplankton Prey in Skaha Lake, British Columbia. North Am J Fish Manag 41:1246–1273

Hyatt KD, Ogden A, Stockwell MM (2018b) Impacts of the 2010 Testalinden Dam Breach on Aquatic Food Webs and Planktivores (Oncorhynchus nerka and Mysis diluviana) at Osoyoos Lake. The 2018 WA-BC Chapter of AFS Annual Meeting: "40 Years of Fish and Fisheries in the Pacific Northwest". Kelowna, BC, Canada

Hyatt KD, Rankin DP (1999) A habitat based evaluation of Okanagan Sockeye salmon escapement objectives. Canadian Stock Assessment Secretariat Research Document 99/191. Fisheries and Oceans Canada, Nanaimo, BC

Hyatt KD, Rankin DP, Wright H, et al. (In Prep.) "Squeeze play" Responses of Okanagan River juvenile Sockeye salmon to habitat changes driven by high epilimnetic temperature and low hypolimnetic oxygen in Osoyoos Lake, BC

Hyatt KD, Stiff HW (2021) Biophysical impacts of climate change on aquatic biota in the Columbia Basin. Columbia Basin Regional Advisory Committee Webinar Series

Hyatt KD, Stiff HW, Stockwell MM (2020) Historic water temperature (1924–2018), river discharge (1929–2018), and adult Sockeye salmon migration (1937–2018) observations in the Columbia, Okanogan, and Okanagan Rivers. Can. Manuscr. Rep.Fish. Aquat. Sci. 3206: xv + 203 p

Hyatt KD, Stockwell M (2010) Fish and water management tool project assessments: record of management strategy and decisions for the 2006-2007 water year. Can. Manuscr. Rep. Fish. Aquat. Sci. 2913: ix + 65 p

Hyatt KD, Stockwell MM (2019) Chasing an Illusion? Successful restoration of Okanagan River Sockeye Salmon in a sea of uncertainty. In: Krueger CC, Taylor WW, Youn S (eds) From catastrophe to recovery: stories of fish management success. American Fisheries Society, Bethesda, MD, pp 65–100

Hyatt KD, Withler R, Garver K (2019) Review of recent and proposed Okanagan Sockeye salmon (Oncorhynchus nerka) fry introductions to Skaha and Okanagan lakes: history, uncertainties, and implication. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/014. vi + 38 p

Jaeger WK, Scheuerell MD (2023) Return (s) on investment: Restoration spending in the Columbia River Basin and increased abundance of salmon and steelhead. PLoS ONE 18:e0289246. https://doi.org/10.1371/journal.pone.0289246

Jones NE (2010) Incorporating lakes within the river discontinuum: longitudinal changes in ecological characteristics in stream–lake networks. Can J Fish Aquat Sci 67:1350–1362. https://doi.org/10.1139/F10-069

Judson B, Willard C, Stiff HW (2023) Age composition, size, migration timing, and estimation of smolt-to-adult survival of natural-origin Sockeye Salmon (Oncorhynchus nerka) in the Wenatchee River (WA) watershed (1997-2019). Can. Manuscr. Rep. Fish. Aquat. Sci. 3269: xi + 43 p

Mantua NJ, Hare SR, Zhang Y et al. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production*. Bull Am Meteorol Soc 78:1069–1080. 10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2

Marmorek DR, Pickard D, Hall A et al. (2011) Fraser River Sockeye salmon: data synthesis and cumulative impacts. ESSA Technologies Ltd, Vancouver, B.C.

Martins EG, Hinch SG, Cooke SJ, Patterson DA (2012) Climate effects on growth, phenology, and survival of Sockeye salmon (Oncorhynchus nerka): a synthesis of the current state of knowledge and future research directions. Rev Fish Biol Fish 22:887–914. https://doi.org/10.1007/s11160-012-9271-9

Matala AP, Narum SR, Saluskin BP et al. (2019) Early Observations from monitoring a reintroduction program: return of Sockeye salmon to a nursery lake of historical importance. Trans Am Fish Soc 148:271–288. https://doi.org/10.1002/tafs.10133

McClure MM, Holmes EE, Sanderson BL, Jordan CE (2003) A large-scale, multispecies status assessment: anadromous salmonids in the Columbia river basin. Ecol Appl 13:964–989

McDaniels T, Wilmot S, Healey M, Hinch S (2010) Vulnerability of Fraser River Sockeye salmon to climate change: a life cycle perspective using expert judgments. J Environ Manag 91:2771–2780. https://doi.org/10.1016/j.jenvman.2010.08.004

McQueen DJ, Ogden AD, Pham S (2024) Bioenergetics-based estimation of lake-carrying capacity for juvenile Sockeye salmon (Oncorhynchus nerka) in Osoyoos Lake, British Columbia. Fisheries and Oceans Canada: Pacific Biological Station, Nanaimo, B.C

Mueter FJ, Peterman RM, Pyper BJ (2002) Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (Oncorhynchus spp.) in northern and southern areas. Can J Fish Aquat Sci 59:456–463. https://doi.org/10.1139/f02-020

Murauskas J, Hyatt KD, Fryer J et al. (2021) Migration and survival of Okanagan River Sockeye salmon Oncorhynchus nerka, 2012–2019. Anim Biotelemetry 9:1–16

National Marine Fisheries Service West Coast Region (2014) Snake River Harvest Module. NOAA Fisheries, Portland, Oregon

Nehlsen W, Williams JE, Lichatowich JA (1991) Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16:4–21

Ng E, Gardner E, Murauskas J (2023) Sockeye salmon emergence timing using the fish water management tools: comparison of prediction to actual timing. Four Peaks Environmental Science & Data Solutions, Wenatchee, Washington

NOAA Ocean Ecosystem Indicators of Pacific Salmon Marine Survival in the Northern California Current | NOAA Fisheries. https://www.fisheries.noaa.gov/west-coast/science-data/ocean-ecosystem-indicators-pacific-salmon-marine-survival-northern. Accessed 11 Apr 2023

Northwest Power and Conservation Council (2023) Endangered Species Act, Columbia River salmon and steelhead, and the Biological Opinion. https://www.nwcouncil.org/reports/columbia-river-history/endangeredspeciesact/. Accessed 17 Apr 2023

O’Sullivan AM, Alex KI (2024) Establishing present day Sockeye salmon (Oncorhynchus nerka| sćwin) spawning capacity in the highly impacted sq̓awsitkʷ|Okanagan River to guide population conservation and restoration. River Research and Applications. 40(7), 1195–1204. https://doi.org/10.1002/rra.4293

Peterman RM, Dorner B (2011) Fraser River sockeye production dynamics. Cohen Comm Tech Rep. 10:1–133

Plourde S, Galbraith P, Lesage V et al. (2013) Ecosystem perspective on changes and anomalies in the Gulf of St. Lawrence: a context in support of the management of the St. Lawrence beluga whale population. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/129. v + 29 p

Quinn, T.P. (2018) The Behavior and Ecology of Pacific Salmon and Trout, 2nd edn. University of Washington Press

R Core Team (2022) R: A language and environment for statistical computing

Riebe CS, Sklar LS, Overstreet BT, Wooster JK (2014) Optimal reproduction in salmon spawning substrates linked to grain size and fish length. Water Resour Res 50:898–918. https://doi.org/10.1002/2013WR014231

Rodionov S (2004) A sequential algorithm for testing climate regime shifts. Geophysical Research Letters 31: https://doi.org/10.1029/2004GL019448

Rodionov S (2005) A brief overview of the regime shift detection methods. Large-scale disturbances (regime shifts) and recovery in aquatic ecosystems: challenges for management toward sustainability 17–24

Rodionov S, Overland JE (2005) Application of a sequential regime shift detection method to the Bering Sea ecosystem. ICES J Mar Sci 62:328–332

Ruggerone GT, Connors BM (2015) Productivity and life history of Sockeye salmon in relation to competition with pink and Sockeye salmon in the North Pacific Ocean. Can J Fish Aquat Sci 72:818–833

Ruggerone GT, Springer AM, van Vliet GB et al. (2023) From diatoms to killer whales: impacts of pink salmon on North Pacific ecosystems. Mar Ecol Prog Ser 719:1–40

Schuett-Hames D, Conrad B, Pleus A, Lautz K (1996) Literature review and monitoring recommendations for salmonid spawning gravel scour. Northwest Indian Fisheries Commission and Washington Department of Fish and Wildlife, Olympia, WA

Simmatis B, Jeziorski A, Zemanek A et al. (2018) Long-term reconstruction of deep-water oxygen conditions in Osoyoos Lake (British Columbia, Canada): implications for Okanagan River Sockeye salmon. Lake Reserv Manag 34:392–400. https://doi.org/10.1080/10402381.2018.1488779

Skalski JR, Whitlock SL, Townsend RL, A. Harnish R (2021) Passage and survival of juvenile salmonid smolts through dams in the Columbia and snake rivers, 2010–2018. North Am J Fish Manag 41:678–696. https://doi.org/10.1002/nafm.10572

Slaney TL, Hyatt KD, Northcote TG, Fielden RJ (1996) Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries 21:20–35

Stockwell MM, Hyatt KD (2003) A summary of Okanagan Sockeye salmon (Oncorhynchus nerka) escapement surveys by date and river segment from 1947 to 2001. Can Data Rep Fish 1106:34

Suter G, Cormier S, Barron M (2017) A weight of evidence framework for environmental assessments: inferring qualities. Integr Environ Assess Manag 13:1038–1044. https://doi.org/10.1002/ieam.1954

Swanson HA (2019) An unexpected politics of population: salmon counting, science, and advocacy in the Columbia River Basin. Curr Anthropol 60:S272–S285. https://doi.org/10.1086/703392

Tannant DD, Skermer N (2013) Mud and debris flows and associated earth dam failures in the Okanagan region of British Columbia. Can Geotech J 50:820–833

Thomson RE, Beamish RJ, Beacham TD et al. (2012) Anomalous Ocean conditions may explain the recent extreme variability in Fraser River Sockeye salmon production. Mar Coast Fish 4:415–437. https://doi.org/10.1080/19425120.2012.675985

Vert-Pre KA, Amoroso RO, Jensen OP, Hilborn R (2013) Frequency and intensity of productivity regime shifts in marine fish stocks. Proc Natl Acad Sci 110:1779–1784

Volkman JM (1996) The endangered species act and the ecosystem of Columbia River salmon. Hastings W-Nw J Envt'L L Pol'y 4:51

Walters CJ, LeBlond P, Riddell B (2004) Does over-escapement cause salmon stock collapse? Pacific Fisheries Resource Conservation Council

Widener DL, Faulkner JR, Smith SG et al. (2018) Survival estimates for the passage of spring-migrating juvenile salmonids through Snake and Columbia river dams and reservoirs, 2017. NOAA Fish Ecology Division, Northwest Fisheries Science Center, Seattle, Washington

Williams JG (2008) Mitigating the effects of high-head dams on the Columbia River, USA: experience from the trenches. Hydrobiologia 609:241–251. https://doi.org/10.1007/s10750-008-9411-3

Williams JG, Smith SG, Fryer JK et al. (2014) Influence of ocean and freshwater conditions on Columbia River Sockeye salmon Oncorhynchus nerka adult return rates. Fish Oceanogr 23:210–224. https://doi.org/10.1111/fog.12056