Animal Biotelemetry

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Migration and survival of Okanagan River Sockeye Salmon *Oncorhynchus nerka*, 2012–2019

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Abstract

Background: Okanagan River Sockeye Salmon *Oncorhynchus nerka* (Okanagan Sockeye) are one of two remaining self-sustaining Sockeye Salmon populations in the Columbia River Basin. We used detection histories of smolts implanted with passive integrated transponder (PIT) tags between 2012 and 2019 to estimate survival and behavioral metrics during reintroduction efforts and changing environmental conditions over the monitoring period.

Results: Smolts migrating to McNary Dam, whose route includes 130 km of the Okanagan River and 388 km of the Columbia River, generally had high survival (mean of 87.0% per 100 km) and fast migration speeds (up to 50 km/day) relative to other salmonids in the region. Smolt-to-adult returns (SARs) ranged from 0.4 to 6.1% and were greater for fish originating from Skaha Lake compared to cohorts tagged in Osoyoos Lake. Most adults returned after 2 years in the ocean (69%), followed by jacks (27%), and adults that spent 3 years at sea (4%), though Skaha Lake adults had a significantly younger age structure than cohorts from Osoyoos Lake. Survival of adults from Bonneville Dam (rkm 235) upstream to Wells Dam (rkm 830) was generally high (80–92%), and migration speed decreased in upstream reaches. Survival from Wells Dam to the Okanagan River was only estimable in 2018, where 64% of adults survived to the spawning grounds. The upstream migration of adult Okanagan Sockeye was significantly compromised during the drought of 2015 when less than 5% of Okanagan Sockeye that returned to the Columbia River reached spawning grounds.

Conclusions: Our results indicate that Okanagan Sockeye have exceptional survival and migratory ability relative to other salmonids, though poor ocean conditions combined with warming water temperatures in freshwater habitats in recent years have the potential to devastate the population. The success of reintroduction efforts to increase spatial structure and diversity of Okanagan Sockeye is, therefore, critical to maintaining the population in years to come.

Keywords: Sockeye Salmon, PIT tags, Columbia River Basin, Survival

Background

Okanagan River Sockeye Salmon *Oncorhynchus nerka* (Okanagan Sockeye) originating from Osoyoos Lake (Canada), and Lake Wenatchee Sockeye Salmon (United States) comprise the last two self-sustaining populations of anadromous *O. nerka* among several that formerly inhabited the Columbia River Basin. Sockeye Salmon once existed in eight Columbia River tributaries, including at least 12 nursery lakes above the Snake River confluence [21, 24, 47], and peak returns likely ranged from 2.5 to 3.2 million adults [12, 21]. Degradation of and blocked access to habitat, urban and industrial development, and overexploitation have greatly diminished returns [27, 36], and by the late 1900s, Columbia River Sockeye Salmon had been virtually extirpated except for populations in the Okanagan (spelled Okanogan in the

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U.S.) and Wenatchee River basins [21, 29, 47]. Despite ongoing threats, Okanagan Sockeye have demonstrated perhaps the greatest recovery of any salmonid population in the Pacific Northwest as returns have increased by an order of magnitude over the last 30 years. Mean counts at Wells Dam increased from 17,083 adults during the 1990s to 199,907 adults during the 2010s [13]. The recovery is largely a response to water resource management in the Okanagan Basin, increased smolt survival through hydroelectric projects, a period of favorable ocean conditions, and the Skaha Lake reintroduction program, including the kł cp̓əlk̓ stim̓ Hatchery in Penticton, British Columbia [33, 69].

While Okanagan Sockeye have demonstrated exceptional resilience, anthropogenic actions continue to influence the population at all life stages. Urbanization, agricultural operations, and water quality and quantity in spawning and early rearing habitats still dominate management discussions; although, anticipating risks to the species has become increasingly complicated under increasing water temperatures [50]. For example, more than 90% of Okanagan Sockeye that entered the Columbia River did not survive to the spawning grounds during record high water temperatures observed in 2015 [22, 34, 38]. The effects of the 2015 drought persisted through 2019 when the dominant year class of that brood year returned at roughly 25% of the recent 10-year average [11]. With temperatures expected to continue increasing in the Columbia River Basin [71], supporting the recovery of imperiled Pacific Salmon stocks is a critical goal of water management agreements between the United States and Canada [15, 53] and litigation concerning hydroelectric development in the Columbia River [1].

Within the commonly referenced Viable Salmonid Population (VSP) framework, the persistence of salmonid populations is characterized in terms of their abundance, productivity, spatial structure, and diversity [48]. Okanagan Sockeye have reached record levels of abundance and productivity, but the lack of spatial structure and diversity presents risk to the population, especially with increases in water temperatures observed in recent years. Habitat in the upper Okanagan River Basin became inaccessible to anadromous fishes following construction of several dams in the 1900s that blocked access to Vaseux Lake (McIntyre Dam, 1921), Skaha Lake (Okanagan Falls Dam, 1958), and Okanagan Lake (Penticton Dam, 1915; Fig. 1). Most of the 20th-century spawning and rearing habitat of Okanagan Sockeye in the Okanagan River Basin [57] was, therefore, restricted to approximately 20 km of the Okanagan River near Oliver, British Columbia, and Osoyoos Lake [33]. Most juvenile Okanagan Sockeye rear in portions of Osoyoos Lake, where increasing water temperatures of the epilimnion

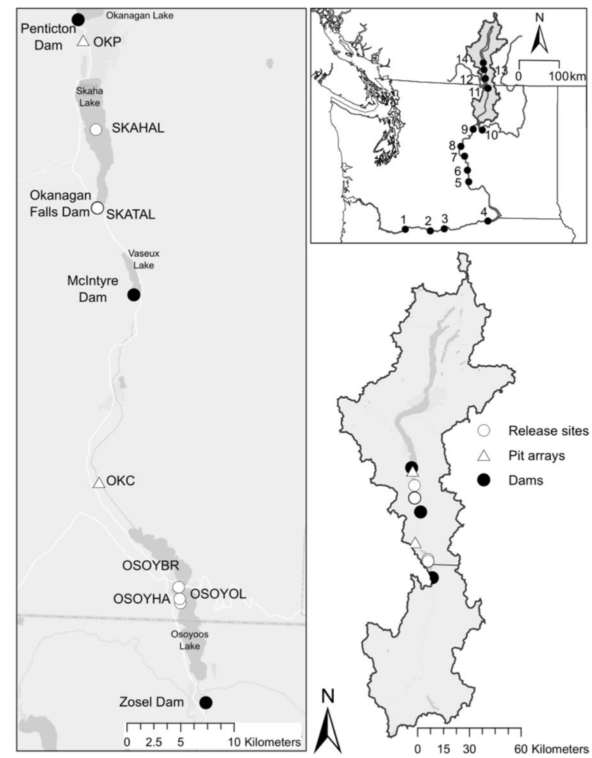

Fig. 1 Overview of the Columbia River migratory corridor (top right); the Okanagan River Basin (bottom right); and juvenile release sites (open circles), PIT arrays (open triangles), and dams (closed circles) in the Okanagan River Basin (left). Dams passed during migration include (1) Bonneville, (2) The Dalles, (3) John Day, (4) McNary, (5) Priest Rapids, (6) Wanapum, (7) Rock Island, (8) Rocky Reach, (9) Wells, (11) Zosel, (12) McIntyre, (13) Skaha, and (14) Penticton dams. Chief Joseph Dam (10) is shown for reference but does not have upstream passage facilities

and decreasing hypolimnetic oxygen concentrations resulting from anthropogenic eutrophication greatly reduce suitable nursery habitat for juveniles during late summer each year [61]. This situation emphasizes the importance of interventions to increase the diversity and spatial structure for Okanagan Sockeye.

Beginning in the late 1990s, efforts to reintroduce Okanagan Sockeye to historical spawning and rearing habitat in the upper Okanagan River Basin was initiated by a diverse group of stakeholders led by the Okanagan Nation Alliance, a First Nations Council in Canada, with critical support from Fisheries and Oceans Canada (DFO), public utility districts in the United States, and the Habitat Conservation Trust Foundation. Reintroduction of Okanagan Sockeye into Skaha Lake commenced in 2004 [9]. By the 2010s, up to 10% of adult returns to the Okanagan River Basin comprised hatchery-origin fish released as fry from the newly constructed the kł cp̓ᵊlk̓ stim̓ Hatchery and upstream passage was improved or reestablished at McIntyre Dam below Vaseux Lake (2009) and Okanagan Falls Dam below Skaha Lake (2011) [33]. To track the success of these efforts, a monitoring and evaluation program was implemented in 2005. Okanagan Nation Alliance staff later worked to create an extensive passive integrated transponder (PIT) tag monitoring network through the freshwater migration corridor. The combined efforts to protect, enhance, and monitor Okanagan Sockeye have proven critical to successful management of one of the most culturally, ecologically, and economically important fisheries in the Interior Columbia River Basin.

The purpose of this manuscript is to provide the first comprehensive analysis of the migration behaviors and population dynamics of Okanagan Sockeye based on data from juveniles that were PIT-tagged and released in the Okanagan Basin. These data may be used to provide estimates of smolt survival during the downstream migration, age-at-maturity, smolt-to-adult returns (SARs), conversion rates of adults during the upstream migration, and a variety of related behavioral metrics, such as travel time and date of arrival [4, 9, 52]. Results presented here will provide survival estimates and other data across critical life stages that can be used to inform recovery strategies that optimize measures in the VSP framework. Specifically, smolt survival, SARs, and adult conversion rates to spawning habitat exert profound influences on salmon abundance and productivity. In addition, behavioral information and survival of Okanagan Sockeye originating from re-established habitat are critical to plans to improve spatial structure and diversity of the population. Finally, recommendations for expanding the current monitoring framework are provided so managers can understand how to best allocate limited resources as conservation efforts evolve in coming years.

Methods

Study area

The Okanagan River is a major tributary to the Columbia River and has an approximate length of 185 km (37 km Canadian section, 148 km United States section). Wild-origin Okanagan Sockeye spawn primarily in the river between Osoyoos and Skaha lakes (Fig. 1) during October [62]. Fry emerge from late April to early May and generally spend 1 year rearing in Osoyoos Lake, and/or the Okanagan River before emigrating as smolts [7, 33]. Hatchery- and, more recently, wild-origin smolts that rear in Skaha Lake pass through Okanagan Falls Dam, continuing their journey down the Okanagan River through McIntyre Dam and Osoyoos Lake (Fig. 1). Okanagan Sockeye smolts from both lakes begin their outmigration at similar times (April–May). Smolts travel downstream and pass through the Osoyoos Lake Narrows, which connects the central and north basins of the lake. From Zosel Dam at the outlet of Osoyoos Lake, the Okanagan River flows south through the United States, converging with the Columbia River near Brewster, Washington, in the reservoir created by Wells Dam. Smolts then migrate through nine hydroelectric projects along the Columbia River to reach the Pacific Ocean (Fig. 1). Okanagan Sockeye then spend anywhere from 1 to 3 years in the ocean before returning to migrate up the Columbia River to spawning grounds in the Okanagan River.

Tagging methods and release sites

Okanagan Sockeye smolts were captured and PIT-tagged at five sites from 2012 to 2019 within the Okanagan River Basin to measure juvenile outmigration survival and travel time from release site to McNary Dam, SAR from the release site back to Bonneville Dam, and adult survival and travel time upstream from Bonneville Dam through the Columbia and Okanagan rivers. Tagging and release sites were identified by codes designated by the Columbia Basin PIT Tag Information System (PTAGIS; www.ptagis.org), and included: Osoyoos Lake (OSOYOL), Osoyoos Lake at Haynes Point Campground (OSOYHA), Osoyoos Lake Narrows Highway 3 Bridge (OSOYBR), the tailrace approximately 0.5 km downstream of Skaha Dam (SKATAL), and Skaha Lake (SKAHAL) (Fig. 1). Fish labeled as released at SKA and SKATAL sites were pooled in each year as this was the same release site. Smolts were captured using either fyke nets, rotary screw traps, purse seines, or a combination at each site over the study years (Table 1). From 2013 to 2017, all or a portion of smolts from Osoyoos Lake were captured using a floating fyke net at the OSOYBR site (see methods in 2). Starting in 2017 purse seine methods were primarily used in all Osoyoos sites [20]. An 8.5 m purse seiner fishing with 183 m seine net (1.27 cm knotted mesh) was used to capture smolts at all Osoyoos Lake and SKAHAL sites from 2016 to 2019. Purse seines fished to a depth of 12 m, concentrating in the central basin of Osoyoos Lake and in the southern region of Skaha Lake where most Okanagan Sockeye smolts congregate. From 2012 to 2016, smolts emigrating from Skaha Lake were captured using two rotary screw traps that operated intermittently throughout the outmigration period [19] downstream of Okanagan Falls Dam. The success of the program resulted in the increase of target number of PIT-tagged smolts from a combined total of 5,000 for Osoyoos and Skaha lakes to 5,000 for each lake (Table 1) [70].

Smolts were anesthetized using a 40 mg/l solution of tricaine methanesulfonate (MS-222) and tagged with Biomark HPT 12 PIT tags (134.2 kHz; 12 mm length)

Table 1 Number of PIT-TAGGED Okanagan Sockeye by PTAGIS release site code, capture method, and release year (2012–2019)

Year	OSOYOL	OSOYHA	OSOYBR		SKA + SKATAL	SKAHAL	TOTAL
	Purse seine	Purse seine	Fyke net	Purse seine	Screw trap	Purse seine	Combined
2012					534		534
2013			2783		1203		3986
2014			3706		1348		5054
2015			1741		5435		7176
2016	3044		1754		3101	2338	10,237
2017	8794		152	2,642			11,588
2018	1521	3562				5860	10,943
2019	4968					4114	9082

OSOYBR Osoyoos Lake Narrows Highway 3 Bridge, *OSOYHA* Osoyoos Lake at Haynes Point Campground, *OSOYOL* Osoyoos Lake, *SKA + SKATAL* Tailrace of Skaha Dam, *SKAHAL* Skaha Lake

according to procedures outlined by PTAGIS and Biomark [2]. Tags were implanted with an MK-25 Rapid Implant Gun along with APT12 pre-loaded needles (Biomark, Boise, Idaho). In addition to receiving a PIT tag, a proportion of smolts were measured for fork length (mm) each year. Following tagging, all mortalities were removed from the tagged population. Visible determination of hatchery versus wild origin was not possible because hatchery Okanagan Sockeye were released as fry when adipose clips were not possible. Therefore, fish origin was not considered in estimation of survival and travel times.

Detection sites for juveniles and adults

Juvenile survival, detection probabilities, and travel time estimates were based on detections of Okanagan Sockeye from release sites to McNary Dam (Table 1). McNary Dam was used as the first point of detection for travel time and survival estimates because it is most capable of providing reasonably precise estimates of survival over the greatest distance of the juvenile freshwater migration corridor. During their downstream migration, smolts pass a maximum of four diversion dams in the Okanagan River before reaching the Columbia River, where they then pass five hydroelectric projects (Wells [river kilometer, rkm 830], Rocky Reach [rkm 762], Rock Island [rkm 730], Wanapum [rkm 669], and Priest Rapids [rkm 639]) before reaching McNary Dam (rkm 470). After McNary Dam, juveniles pass through John Day (rkm 347), The Dalles (rkm 308), and Bonneville (rkm 235) dams before reaching the Pacific Ocean (rkm 0). The farthest downstream detection site was in the Columbia River estuary, where the National Marine Fisheries Service operated a paired-trawl detection system [44].

Survival and travel time of adult Okanagan Sockeye migrating through the Columbia River and Okanagan River back to their spawning grounds was based on detections of PIT-tagged adults at various points. The first detection site through which all adult Okanagan Sockeye must pass along their return migration are the fish ladders at Bonneville Dam. These detection points (PTAGIS Site Code) include arrays in the Bradford Island Ladder (BO1), Bonneville Cascades Island Ladder (BO2), Bonneville WA Shore Ladder (BO3), and Bonneville WA Ladder slots (BO4). The next upstream detection site used in this study is McNary Dam where PIT-tagged adults are detected at the McNary Oregon Shore Ladder (MC1) or McNary Washington Shore Ladder (MC2). Continuing into the upper Columbia River from McNary Dam, the next upstream site used in this study is Wells Dam where adults are detected at the Adult Ladders (WEA). After passing Wells Dam, Okanagan Sockeye travel up the Okanagan River where the first adult PIT-tag detection site used in this evaluation is at Okanagan Channel at Vertical Drop Structure-3 (OKC), installed in 2009 (Fig. 1). The last upstream detection point in the Okanagan River Basin, the Penticton Channel PIT array (OKP), was installed and operational in 2018.

Juvenile survival, detection probabilities, and travel time analyses

Survival, detection probabilities, and travel time of Okanagan Sockeye smolts were estimated for each PIT-tagged release group to McNary Dam (2012–2019; Table 1). Estimates of juvenile survival and travel time were generated from the Columbia River Data Acquisition in Real Time (DART) query program [13]. The DART query retrieves PIT-tag data files of individual-based capture history from PTAGIS (for tag files used see Additional file 1: Appendix S1) and uses these files to generate survival estimates, detection probabilities, and travel times for each release site in each year. Survival estimates, detection probabilities, and associated standard error for each release group in each year were estimated in DART using the Cormack–Jolly–Seber (CJS) model [14, 40, 60]. Assumptions for the CJS model include (1) individuals marked for the study are a representative sample from the population of interest; (2) survival and capture probabilities are not affected by tagging or detection; (3) all detections are instantaneous; (4) the fate of each tagged individual is independent of the fate of all others; (5) all tagged individuals alive at the beginning of a reach have the same probability of surviving until the end of that reach; (6) all tagged individuals alive at the beginning of a detection site have the same probability of being detected at that site; (7) each individual detected at a particular detection site has the same probability of being removed, and (8) the probability of removal is independent of the survival process. Data files containing records from all Okanagan release sites from PTAGIS were examined for erroneous records, inconsistencies, and anomalies. Data files of releases of juvenile Okanagan Sockeye in Osoyoos Lake (OSOYOL, OSOYOHA, and OSOYBR) and Skaha Lake and Skaha Dam tailrace (SKA, SKATAL, and SKAHAL) since 2012 were analyzed. Survival estimates were not adjusted for juveniles that did not emigrate, tag failure, tag loss, or other factors, which could result in fish surviving but not being detected at a downstream location. Due to these factors, actual survival may be higher than the reported estimates.

Survival estimates across all years and sites were used in a regression-model framework to better understand the factors associated with juvenile survival. Multiple weighted logistic regression was used to explore how variation in juvenile survival is explained by outmigration year, release site, release date, and smolt size (i.e., average length). The modeling framework followed Eq. (1):

$$logit(p_i) \sim \beta_0 + \sum_{k=1}^{p} \beta_k x_k + \varepsilon_i, \varepsilon_i \sim N\left(0, \sigma^2\right) \quad (1)$$

where p_i is the probability of juvenile survival observed across all individuals from group i (i = 1, ..., 18); β_0 is the intercept; β_{k} is the weighted slope term for each covariate x_{k}; ε_i is the normally distributed random error associated with group i.

Each observation was weighted using the number of individuals within the release group (i.e., $w_i = n_i$), and these weights were used to adjust the covariance matrix to give higher weights to those site and year combinations where the number of smolts was highest. Forward selection based on AICc [8] was used to find the most parsimonious model amongst a suite of candidate models, including outmigration year, release site, release date, and smolt length. Two out of 18 release groups were initially lacking length data: individuals released from Skaha Dam (SKA + SKATAL) in 2015 and individuals released from Skaha Lake (SKAHAL) in 2019. Because these omissions appeared random across years for each release site, we interpolated average length for these releases groups by averaging values across years where length data were present from the same site (SKA + SKATAL: n = 4, standard deviation 3.21 mm; SKAHAL: n = 2, standard deviation 5.21 mm.) Exploratory analyses were conducted prior to model fitting to ensure distributional assumptions were met and to avoid issues in multi-collinearity [72]. All modeling and validation were conducted in R (v. 3.6.1, R Core Team 2019).

Travel-time estimates were based on the release date for each PIT-tagged fish and the first detection date at McNary Dam. Harmonic mean travel time was used to describe each group's (by release site and year) rate of travel from release site to McNary Dam. This statistical summary of central tendency is more robust to the presence of outliers (i.e., a very fast or slow fish) than arithmetic mean and is computed following Eq. (2):

$$\widehat{t} = \frac{n}{\sum_{i=1}^{n} \frac{1}{t_i}} \quad (2)$$

where $\widehat{t}$ is the computed harmonic mean travel time; n is the observed number of unique fish detected at the detection sites; t_i is the observed reach travel time for each fish i through n.

Smolt to adult survival rates and proportion of ocean-age adults returning

Smolt-to-adult survival rates (SARs) and associated standard errors were calculated as the number of PIT-tagged smolts released from each lake of origin (Skaha Lake or Osoyoos Lake) in each year (2012–2016) that survived to return as adults to Bonneville Dam as ocean age-1, age-2, or age-3 adults in 2013–2019. This approach assumes that smolts emigrate to the ocean the year they are tagged and is supported by the negligible proportion of smolts that hold over an additional year following tagging [23]. PIT-tagged fish released in years 2017–2019 were excluded from the analysis due to incomplete age-structure data sets (i.e., return data only includes through 2019; therefore, no age-2 and age-3 data are available for 2018 and 2017, respectively) and small sample sizes in those years. Data used in the analysis were queried using the PTAGIS interrogation summary tool. A query reporting all instances of Okanagan Sockeye detected at the Bonneville adult ladders (BO1, BO2, BO3, and BO4) from each release site and each year was generated. Bonneville Dam provides the first points of detection for all adults as they begin their upriver migration to spawning grounds and has nearly 100% detection efficiency when pooling data from the four PIT-tag interrogation sites [63]. Duplicate tag numbers were deleted from each data set to eliminate duplicate detections within each detection site. All data from the PTAGIS interrogation summaries were examined for erroneous records, inconsistencies, and anomalies. The equation used to calculate SAR for each basin release group for each year across all ages of adults returning (SAR_{ij}) is provided in the following equation:

$$SAR_{ij} = \frac{A_{ij}}{R_{ij}} \quad (3)$$

where A_{ij} is the total number of adults originating from either Skaha or Osoyoos lakes and detected at Bonneville Dam (i) in each year (j); R_{ij} is the total number of juveniles released from each lake (i) in each year (j).

Data were further analyzed to determine length of time of ocean residence to calculate proportion of ocean age-1, age-2, and age-3 Okanagan Sockeye that return to Bonneville Dam. Ocean age was determined by subtracting year of release from year of return. A Chi-squared test was conducted to determine whether proportions differed by return year and tagging basin.

Adult upstream survival estimates, detection probabilities, and travel time

Survival estimates and detection probabilities for adult Okanagan Sockeye migrating upstream through the Columbia to the Okanagan River Basin were calculated using a mark–recapture model in MARK [67]. Adults pass through several dams with detection arrays on the way back to their spawning grounds. In this analysis, adult survival rates and detection probabilities were calculated using detections from Bonneville Dam to McNary Dam to Wells Dam to OKC to OKP. Survival rates were calculated by migration reach and year that adults returned, so results did not examine effect of juvenile release site, year-class strength of juveniles, or age-specific survival (juvenile or adult). In addition, survival rates did not account for differences in detection probability estimates that manifested across years at various sites. OKP was installed in 2018, so data were only available for 2018 and 2019 for this site. Because survival estimates rely on detecting an individual at the site beyond the site of interest, survival estimates to OKC were only possible in 2018 and 2019. Data obtained from PTAGIS were examined for erroneous records, inconsistencies, and anomalies. All adult records where individuals were detected only at Wells Dam, OKC, and OKP (and not at Bonneville or McNary dams) were eliminated from analysis ($N = 33$) because Bonneville and McNary dams collectively have near-perfect detection rates and these individuals are almost certainly resident *O. nerka* (i.e., kokanee). Included in these 33 samples were eight fish detected only at OKP in 2019; these fish were not included in calculations of survival estimates. Survival estimates of adults returning to OKC were, therefore, only possible in 2018 due to lack of data or exclusion of individuals that were not confirmed to emigrate to the ocean. An additional 180 individuals were eliminated from the analysis because they were juveniles detected in adult fishways during the year of release as smolts. A total of 395 adult Okanagan Sockeye were ultimately used in the mark–recapture analysis to estimate adult survival and detection probabilities upstream through the Columbia River to the Okanagan River Basin.

Our analysis relied on survival rates derived in a mark–recapture framework to understand important factors driving juvenile survival. Parameter estimation proceeds by first estimating detection probabilities, and then using these estimates to provide an estimate of survival probability based of apparent detection. Therefore, our survival probabilities were sensitive to differences in detection efficiency across years and sites and were thus likely affected by factors that can influence detection efficiency (e.g., flow). Although a more robust approach would include covariates within a mark–recapture framework to estimate their contribution to detection and survival probability, we took this opportunistic approach to understand how various geographic, morphological, and phenological factors impacted a decent estimate of survival.

Adult return data through the Columbia and Okanagan rivers were examined to determine whether median day of arrival at each dam and travel time from Bonneville to McNary, McNary to Wells, and Wells to OKC varied across years (2013–2019); basin of origin (Skaha Lake and Osoyoos Lake) was also examined. Data were queried from PTAGIS using an interrogation summary. Adult and juvenile data were returned from the interrogation summary; all juvenile data were eliminated from analysis. Travel time was standardized to distance by calculating kilometer per day traveled for each PIT-tagged fish and averaging across each reach: Bonneville to McNary Dam (236 km), McNary to Wells Dam (360 km), and Wells Dam to OKC (177 km). Travel time was calculated from date of last detection at downstream detection site to date of last detection at upstream detection site. To test whether arrival date at each dam detection site (Bonneville, McNary, Wells, OKC) differed by year and by lake of origin, a separate Wilcoxon test was conducted for year and lake. Median migration speed (km/day) between each detection site was calculated for all returning adults. A Wilcoxon Rank Sum test was conducted to examine whether all returning adults traveled at different speeds

Table 2 Regression coefficients, standard errors, and associated *P* values for the full model estimating juvenile survival against release year, release site, average length, and release date

Predictor	Coefficient	Standard error	*p*
Intercept	− 4.85	0.48	< 0.01
2013	− 0.88	0.10	< 0.01
2014	− 1.38	0.10	< 0.01
2015	− 1.15	0.10	< 0.01
2016	− 0.54	0.12	< 0.01
2017	− 0.87	0.11	< 0.01
2018	− 0.46	0.11	< 0.01
2019	− 1.14	0.11	< 0.01
SKA + SKATAL	0.01	0.09	0.90
OSOYBR	1.06	0.06	< 0.01
OSOYHA	1.19	0.07	< 0.01
OSOYOL	0.89	0.05	< 0.01
Average Length	0.02	< 0.01	< 0.01
Release Date	0.03	< 0.01	< 0.01

Release date was omitted in the final model based on AIC. Coefficients are given as raw values in log-odds space. *P* values represent the significance test result using the corresponding Wald's statistic

between each detection site and to determine whether fish originating from Skaha or Osoyoos lakes exhibited different migration speeds between detection sites. Differences were considered significant at $p = 0.05$.

Results

Juvenile survival and travel time

Following model selection, the model containing year, release site, and average length was the most parsimonious in explaining juvenile survival from release site to McNary Dam, while release date was not found to be a significant predictor of survival. This model was selected from the next best candidate model with ΔAICc = 21.72, and was found to significantly reduce deviance compared to the null model ($\chi^2_{12} = 4,698.6, p < 0.01$). Regression coefficients were found to be largely significant at the α = 0.01 level (Table 2). Coefficients to the log odds suggested variable juvenile survival success across years and sites (Fig. 2). Smolts emigrating in 2014 and 2015 performed poorer than those emigrating in 2017 and 2018. In addition, juveniles released from the OSOYBR site fared far better than those from other sites—individuals released from OSOYBR had odds of about 4.77-to-1 of surviving (95% CI [4.37, 5.21]). Juveniles tagged in Osoyoos Lake had higher survival from release site to McNary Dam in each year compared to fish tagged in Skaha Lake except for 2018 (Table 3; Fig. 3). Greater lengths were associated with greater outmigration success, with a 25 mm increase in length corresponding with a doubling of the odds of survival (Fig. 2). Except in 2013, when travel time was equal, juvenile Okanagan Sockeye released from Skaha Lake traveled faster to McNary Dam than those released from Osoyoos Lake sites in all years, despite traveling a farther distance (migration distance

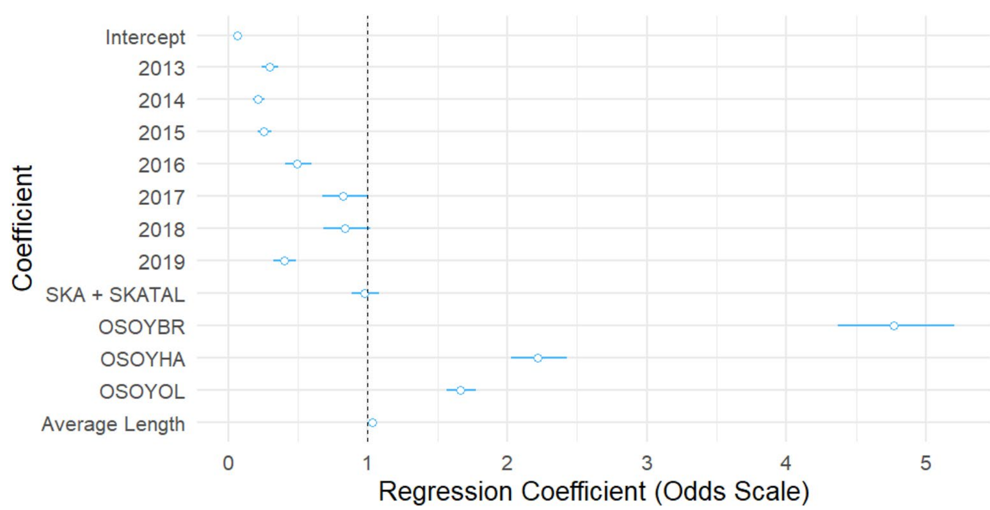

Fig. 2 Regression model coefficients for the selected final model summarizing relationships of observed juvenile survival to predictors. All results are transformed to the logarithmic odds scale. Lines indicate the 95% confidence interval for the regression coefficient, as calculated through the transformed Wald's statistic. The intercept of the model represents estimated juvenile survival for individuals released from Skaha Lake in 2012. Coefficients for year and release site are offsets to this base survival rate. The vertical line at 1 represents the inflection point between a decrease (less than 1) or an increase (greater than 1) to the default odds of return

Table 3 Survival estimates (and standard error) of groups of PIT-tagged juvenile Okanagan Sockeye from release site in the Okanagan River Basin to McNary Dam by release year (2012–2019)

Year	Release site (by distance)				
	OSOYOL	OSOYHA	OSOYBR	SKA + SKATAL	SKAHAL
2012	NA	NA	NA	0.64 (0.23)	NA
2013	NA	NA	0.50 (0.12)	0.45 (0.16)	NA
2014	NA	NA	0.44 (0.05)	0.25 (0.06)	NA
2015	NA	NA	0.54 (0.22)	0.29 (0.05)	NA
2016	0.51 (0.09)	NA	0.51 (0.10)	0.40 (0.06)	0.39 (0.08)
2017	0.59 (0.07)	NA	0.97 (0.29)	NA	NA
2018	0.35 (0.08)	0.61 (0.09)	NA	NA	0.53 (0.07)
2019	0.54 (0.09)	NA	NA	NA	0.28 (0.07)

OSOYBR Osoyoos Lake Narrows Highway 3 Bridge, *OSOYHA* Osoyoos Lake at Haynes Point Campground, *OSOYOL* Osoyoos Lake, *SKA + SKATAL* Tailrace of Skaha Dam, *SKAHAL* Skaha Lake

for Skaha Lake sites is approximately 45 km longer than Osoyoos sites). Travel time in 2015 was slower than in other years for smolts originating from both lakes (Table 4).

Survival to maturity

Smolt-to-adult return rates (SARs) to Bonneville Dam ranged from 0.4 to 6.1% across all release years for fish originating from the Okanagan River Basin. SARs were higher for fish tagged in Skaha Lake than for those tagged in Osoyoos Lake for all years (Table 5). SARs varied by year and were highest in release-year 2013 (Skaha = 6.1%, Osoyoos = 3.1%) and lowest in 2015 (Skaha = 0.6%, Osoyoos = 0.4%). Proportion of ocean age-1, age-2, and age-3 fish returning varied by year ($X^2 = 16.1$, $p < 0.01$) and by tagging basin ($X^2 = 32.3$, $p < 0.01$; Fig. 4). Overall, the mean age structure of adult Okanagan Sockeye at Bonneville Dam included 27% ocean age-1, 69% ocean age-2, and 3% ocean age-3. Returning adults were predominantly ocean age-2 for both Skaha- and Osoyoos-origin fish (Fig. 4). There was a higher percentage of ocean age-1 fish returning from Skaha-origin smolts (34%) than from Osoyoos-origin smolts (18%) across all years. Of all years, 2014 had the lowest percentage of ocean age-1 fish returning from either Skaha-origin smolts (11%) or Osoyoos-origin smolts when no ocean age-1 fish returned. Numbers of ocean age-1 fish from Skaha Lake remained low in 2015 (6%), by contrast with age-1 Osoyoos-origin fish that had the highest number of all years (43%).

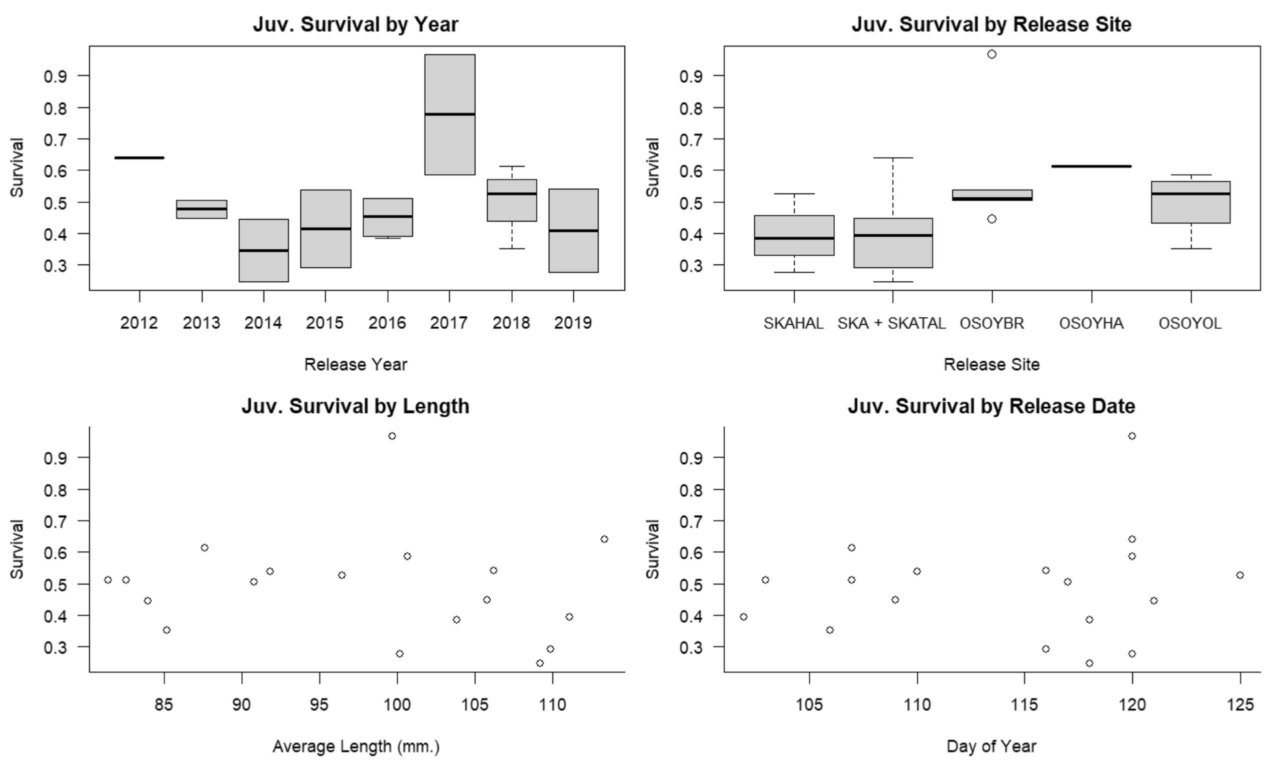

Fig. 3 Relationships between juvenile survival and predictors. Boxplots are shown for categorical variables (release year and site) and scatter plots for continuous variables (average length and release date)

Table 4 Mean harmonic travel time in days (and standard error) of groups of PIT-tagged juveniles from release site in the Okanagan River Basin to McNary Dam by release year (2012–2019)

Year	Release site (by distance)				
	OSOYOL	OSOYHA	OSOYBR	SKA + SKATAL	SKAHAL
2012	NA	NA	NA	11.4 (0.3)	NA
2013	NA	NA	22.8 (0.6)	22.7 (0.6)	NA
2014	NA	NA	20.2 (0.3)	13.3 (0.2)	NA
2015	NA	NA	28.1 (1.0)	20.9 (0.4)	NA
2016	26.6 (0.8)	NA	22.1 (0.7)	17.1 (0.2)	15.9 (0.4)
2017	14.7 (0.2)	NA	14.8 (0.4)	NA	NA
2018	24.7 (0.5)	21.2 (0.2)	NA	NA	13.2 (0.2)
2019	25.8 (0.4)	NA	NA	NA	24.2 (0.6)

OSOYBR Osoyoos Lake Narrows Highway 3 Bridge, *OSOYHA* Osoyoos Lake at Haynes Point Campground, *OSOYOL* Osoyoos Lake, *SKA + SKATAL* Tailrace of Skaha Dam, *SKAHAL* Skaha Lake

Table 5 Smolt-to-adult return rates (SARs) and standard error (SE) in percentages, number of juvenile Okanagan Sockeye released, and number of adult Okanagan Sockeye detected at Bonneville Dam (BON) for each release year (2012–2016) and juvenile release site in the Okanagan River Basin

Year	Release site	# Juveniles released	# Total adults detected at BON	SAR	SE
2012	Skaha	534	26	4.9%	0.93%
2013	Osoyoos	2783	85	3.1%	0.33%
2013	Skaha	1203	73	6.1%	0.69%
2014	Osoyoos	3706	35	0.9%	0.16%
2014	Skaha	1348	28	2.1%	0.39%
2015	Osoyoos	1741	7	0.4%	0.15%
2015	Skaha	5435	35	0.6%	0.11%
2016	Osoyoos	4798	24	0.5%	0.10%
2016	Skaha	5439	55	1.0%	0.14%

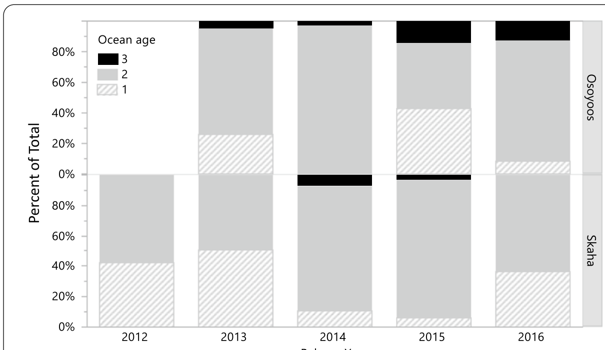

Fig. 4 Proportion of ocean age-1, age-2, and age-3 Okanagan Sockeye adults returning to Bonneville Dam by release year (2012–2016) and juvenile tagging basin (Osoyoos Lake and Skaha Lake) in the Okanagan River Basin

Adult migration

Adult survival of Okanagan Sockeye was estimated from Bonneville Dam to McNary Dam and from McNary Dam to Wells Dam for all adult return years (2013–2019). Due to lack of detections at lower sites of fish also detected at OKP, sample sizes were only sufficient to calculate survival from Wells Dam to OKC in 2018. Detection probabilities ranged from 92 to 100% at Bonneville, McNary, and Wells Dams (Table 6). In most years, as expected, adults traveling from Bonneville to McNary Dam had higher survival than those traveling from McNary to Wells Dam, except in 2015 when McNary to Wells Dam had higher survival and in 2019 when survival was equal between these two reaches. Survival in 2015 was lowest for both reaches. In 2018, Wells Dam to OKC had lower survival than the other two downstream reaches (Table 6).

Arrival dates of adult Okanagan Sockeye to Bonneville Dam, McNary Dam, and Wells Dam were approximately normal (Fig. 5). At these three lower dams, no differences were observed between mean arrival date of fish originating from Osoyoos- and Skaha-origin tag groups ($Z < -0.37$, $p > 0.25$). However, arrival date of adults to OKC exhibited a bimodal distribution with arrival date peaks occurring on July 14 and October 2. Importantly, differences were observed between fish from Skaha versus Osoyoos tag groups at OKC detection site ($Z = 4.84$, $p < 0.01$). Cumulative probability indicates that a portion of Skaha-origin fish arrives at OKC in July, followed by few fish arriving in August and another big pulse in September to early October (Fig. 6). Whereas Osoyoos-origin fish don't start arriving at OKC en masse until mid-September, even though they arrive at similar times to Wells Dam as Skaha-origin fish. Nonparametric pairwise comparisons using the Wilcoxon method indicated that arrival timing to Bonneville, McNary, and Wells dams was not statistically different among years ($p > 0.10$) with exception of 2015 at McNary Dam and 2013 and 2014 at all three detection sites ($p \leq 0.02$). At OKC site, differences were observed among some years; however, representation by tagged Okanagan Sockeye from both lakes of origin was not evenly distributed in those years where differences were observed.

Okanagan Sockeye traveled at different migration speeds between detection sites on the upstream migration from Bonneville Dam ($X^2 = 406.0$, $p < 0.01$). Median migration speed (and 10% to 90% range) decreased as fish moved farther up the Columbia–Okanagan system from Bonneville Dam to McNary Dam, McNary Dam to Wells Dam, and Wells Dam to OKC at 52.0 km/day (39.0 to 63.0 km/day), 36.4 km/day (27.0 to 45.4 km/day), and 2.6 km/day (1.8 to 36.4 km/day), respectively. Because of the large variation in migration speed,

Table 6 Survival estimates with standard error (SE) and detection probabilities with standard error for adult Okanagan Sockeye upstream migration from Bonneville to McNary Dam, from McNary to Wells Dam, and from Wells Dam to the Okanagan detection site (OKC) for 2013–2019

Year	Survival estimates (SE)			Detection probabilities (SE)		
	Bonneville to McNary	McNary to wells	Wells to OKC	Bonneville	McNary	Wells
2013	1.00 (0.00)	0.92 (0.08)	NA	1.00 (0.00)	1.00 (0.01)	NA
2014	0.95 (0.03)	0.79 (0.05)	NA	0.96 (0.02)	1.00 (0.01)	NA
2015	0.60 (0.59)	0.69 (0.06)	NA	0.95 (0.03)	1.00 (0.01)	NA
2016	0.88 (0.04)	0.85 (0.05)	NA	0.98 (0.02)	1.00 (0.00)	NA
2017	0.95 (0.03)	0.80 (0.05)	NA	0.98 (0.02)	1.00 (0.01)	NA
2018	0.85 (0.05)	0.83 (0.05)	0.64 (0.09)	0.95 (0.04)	1.00 (0.00)	0.92 (0.08)
2019	0.95 (0.05)	0.95 (0.05)	NA	1.00 (0.01)	1.00 (0.01)	NA

Survival from Wells to OKC was unavailable prior to installation of the upstream array (OKP) in 2017 and otherwise unestimable due to sample size

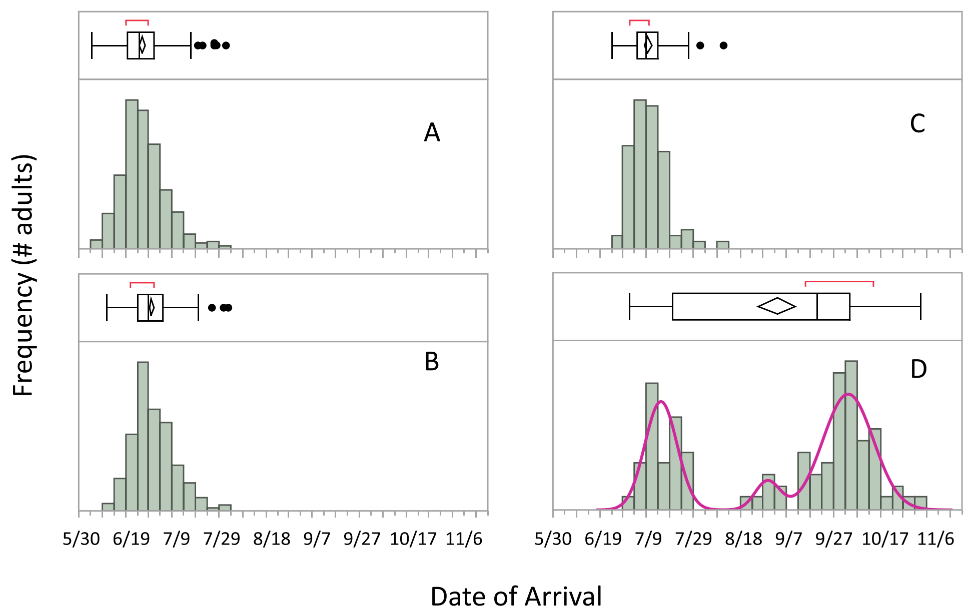

Fig. 5 Frequency of arrival dates of adult Okanagan Sockeye to Bonneville Dam (**A**), McNary Dam (**B**), Wells Dam (**C**), and OKC PIT array (**D**) across all years and tagging basins

specifically between Wells Dam and OKC, data were further compared to examine migration speed among reaches based on which lake of origin (Osoyoos or Skaha Lake) fish were tagged. No difference in migration speed between Osoyoos- and Skaha-origin adults was observed in the Bonneville to McNary Dam reach (Osoyoos $N = 130$, Skaha $N = 182$; $Z = -0.84$, $p = 0.40$) or in the McNary to Wells Dam reach (Osoyoos $N = 99$, Skaha $N = 159$; $Z = -0.13$, $p = 0.89$). However, there were significant differences in migration speed between Osoyoos- and Skaha-origin adults traveling from Wells Dam to OKC (Osoyoos $N = 31$, Skaha $N = 64$; $Z = -5.38$, $p < 0.01$; Fig. 7). Osoyoos-origin fish traveled much slower and with less variation than Skaha-origin fish with median migration speed of 2.0 km/day (1.6 to 3.6 km/day); whereas Skaha-origin fish overall traveled slightly faster with much larger variation with median migration speed of 4.7 km/day (2.0 to 40.8 km/day; Fig. 7).

Discussion

Results from PIT-tagging efforts in the Okanagan River Basin over the 8-year study period provide key insights into survival and behavior of the largest population of Sockeye Salmon in the Columbia River Basin. Estimates of smolt survival during the downstream migration,

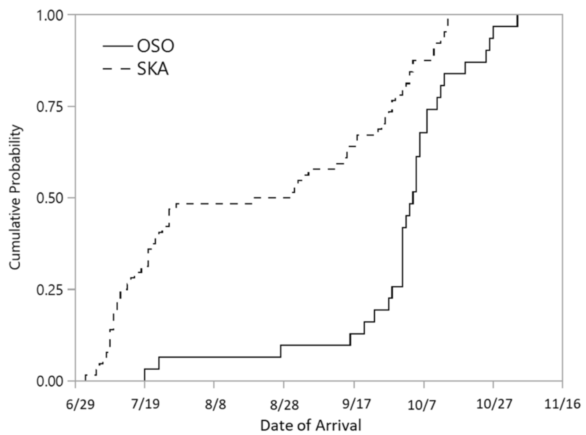

Fig. 6 Cumulative probability of adult arrival date to OKC site from Wells Dam for PIT-tagged adults originating from Skaha Lake (SKA) and Osoyoos lakes (OSO) for all years combined (2013–2019)

SAR and age structure, and upstream conversion rates of adults provide critical information on the viability of the population. The results also highlight extreme variation in survival over a short timeframe in response to changes in ocean conditions and river temperatures during the spawning migration. Each aspect of the analyses is discussed below, including how shifts in environmental conditions affect Okanagan Sockeye. We then compare Okanagan Sockeye originating from Osoyoos and Skaha lakes to underscore the importance of spatial structure, diversity, productivity, and numerical abundance of Okanagan Sockeye. Finally, we recommend minor modifications to monitoring and evaluation efforts that will improve the management of Okanagan Sockeye.

The downstream migration of Okanagan Sockeye smolts is relatively efficient compared to other juvenile salmonids in the Columbia River Basin. For example, travel speeds of yearling Chinook Salmon *O. tshawytscha* have been estimated at 21.5 km/day in the mainstem Columbia River [26]. Travel speed of yearling Chinook Salmon in natal tributaries has been measured at less than 6 km/day [51]. In comparison, travel speed of Okanagan Sockeye smolts through 130 km of Okanagan River and 388 km of Columbia River is generally above 25 km/day. Smolts released in Skaha Lake migrate even faster than those released in Osoyoos Lake, averaging 34 km/day and ranging up to 50 km/day. These observations are comparable or faster than migration speeds in natural and modified systems reported elsewhere [26, 49, 65] and represent an impressive speed greater than 3.0 body lengths per second over an extended distance [3]. Our results are consistent with longstanding characterizations of Sockeye Salmon: smolts leave nursery areas in high numbers over a short period and travel quickly to the ocean [30].

Perhaps more noteworthy is the estimated survival of smolts from release sites in the Okanagan River Basin to McNary Dam. Survival averages 49% across all release groups in our analyses, despite traversing over 130 km in the highly modified Okanagan River and another 388 km of the Columbia River that includes five large-scale hydroelectric projects. This translates to an average survival rate of 87.0% per 100 km (95% CI 84.5 to 89.5%). In comparison, mean survival of Sockeye Salmon smolts from the Sawtooth Valley in Idaho has been estimated between 87.5 and 91.9% per 100 km to the uppermost Snake River hydroelectric project with fish passage (from Alturas, Pettit, and Redfish lakes to Lower Granite Dam, distances of 774, 767, and 750 km, respectively) [28]. Survival of these same populations in the mainstem Snake and Columbia rivers are more comparable (21-year average of 81.1% per 100 km) [68], though lower than Okanagan Sockeye. Sockeye Salmon smolts emigrating from Cultus Lake in the unimpounded Fraser River

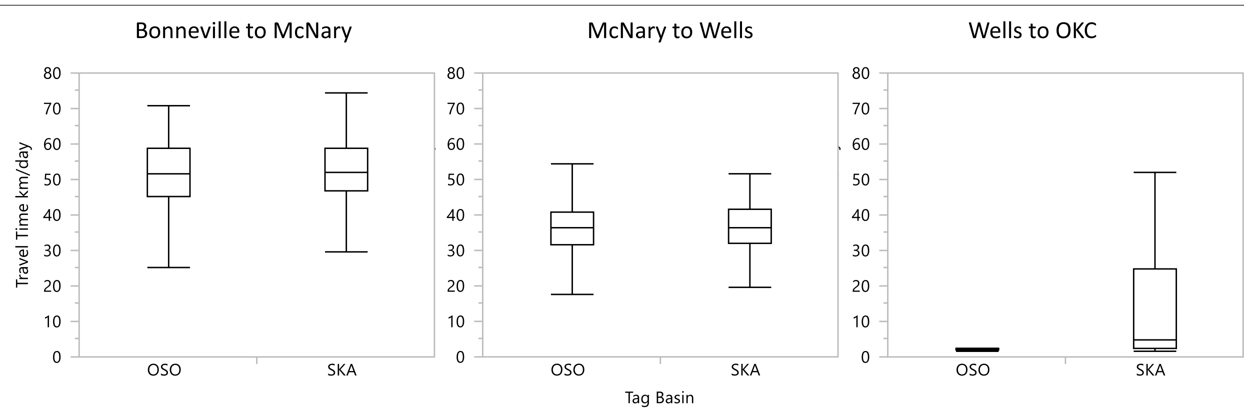

Fig. 7 Box and whisker plot showing migration speed (km/day) of Osoyoos-origin and Skaha-origin adult Okanagan Sockeye traveling from Bonneville Dam to McNary Dam, from McNary Dam to Wells Dam, and from Wells Dam to OKC site combining all years (2013–2019)

have considerably lower survival rates of ≈ 50 to 70% per 100 km over 4 years of monitoring, though different technologies were used in the evaluation [65]. Other salmonids in the region also have lower smolt survival in mainstem [68] or tributary habitats [6]. While these estimates are not directly comparable, they do suggest that Okanagan Sockeye have relatively high rates of survival during the juvenile outmigration.

Like most Sockeye Salmon populations, fish originating from the Okanagan River Basin had a highly variable SAR. Release groups from this study, spanning just 5 years, vary by more than an order of magnitude, from 0.4% (2015 Osoyoos Lake releases) to 6.1% (2013 Skaha Lake releases). These estimates (mean of 2.2%) and previous estimates of Okanagan Sockeye SARs ranging to more than 12% [Kim Hyatt, Department of Fisheries and Oceans Canada, personal communication] are high relative to other populations in the Columbia River Basin. Snake River Sockeye Salmon also traverse over 1,000 km and eight hydroelectric projects during the smolt migration, though SARs have been found to be much lower, at less than 1.0% from 2005 to 2009 [28]. Sockeye Salmon SARs from the Wenatchee River Basin—88 km and two hydroelectric projects downstream of the Okanagan River confluence—ranged from 0.02 to 2.55%, though these are likely biased low based on recent PIT-tag analyses and observations of adults obstructed at trapping facilities below the spawning grounds [31, 52]. In contrast, all Sockeye Salmon originating from the Columbia River Basin (the southern extent of the species) generally have lower SARs compared to stocks in British Columbia or Alaska [39, 43]. However, Sockeye Salmon in the Columbia River Basin are similar to northern counterparts in that ocean conditions combined with broader-scale climate indices are by far the strongest predictors of SARs [64, 69]. The final detection point used in SAR calculations varies among these populations so corrections for distance traveled, harvest, or natural mortality would provide more comparable estimates.

Age structure of Okanagan Sockeye based on this study was mostly consistent with other populations, with most (69%) fish returning to spawn after 2 years at sea and a measurable proportion of jacks (27%) and a few (< 4%) adults that spend 3 years at sea. Age structure was highly variable among years, consistent with previous observations of up to six different age combinations of Okanagan River stocks [22]. In comparison, Wenatchee River Sockeye Salmon have lower diversity in age structure and are comprised entirely of age 4 and 5 adults [22, 31]. Nutrient levels in nursery lakes [62] and conditions during early marine entry are known to influence age at maturity in Sockeye Salmon [55] and likely influenced the years included in our analyses. Given the recent extreme variation in ocean conditions [42] and freshwater environments [17], we suspect that the diversity in age structure of Okanagan Sockeye will be a key aspect of maintaining population viability in the future [48, 59].

Survival of adult Okanagan Sockeye during their upstream migration in freshwater was highly variable and could become the most significant threat to the species if increasing temperature trends continue [38, 46]. Conversion rates of Okanagan Sockeye through the 595 km-reach between Bonneville and Wells dams (i.e., the product of the two reach conversion rates presented in Table 6) ranged from a high of 92% in 2013 to a low of 41% in 2015. This indicates that pre-spawn mortality in the mainstem Columbia River during the 2015 drought exceeded 250,000 adult Okanagan Sockeye. For added context, this loss is roughly equivalent to 11 million smolts over the previous 3 years (based on an average SAR of 2.2%); 360 million eggs in the 2015 brood year; and more than double the number of adult Sockeye Salmon observed returning to the Columbia River between 1995 and 1999 [11]. More concerning is the additional losses that occurred above the hydroelectric system in 2015: only 10,400 of the 187,055 (5.6%) adult Okanagan Sockeye observed passing Wells Dam ultimately reached spawning grounds in the Okanagan River Basin [38]. While survival of adult Okanagan Sockeye during the upstream spawning migration is generally favorable relative to other Columbia River Basin stocks (e.g., Snake River Sockeye Salmon) [16] or other salmonids [5], it is clear that droughts and higher water temperatures pose a tremendous risk to the population.

The most influential condition of variation in spawning escapement of Okanagan Sockeye is the thermal barrier that develops each summer at the confluence of the Okanagan and Columbia rivers near Brewster, Washington (rkm 859), where water temperatures often differ by 10–15 °C in July and August. The barrier was first reported in the 1960s by researchers that were evaluating Sockeye Salmon passage at the newly constructed Rocky Reach Hydroelectric Project (rkm 761) in 1961. Once water temperatures in the Okanagan River exceed 21 °C, Okanagan Sockeye will not enter the tributary, creating delays that can last several weeks [45]. The consequence of this delay was highlighted in 2015, where conversion rates from Bonneville Dam to spawning grounds in 2015 dropped to 4.3% as water temperatures in the Okanagan River remained at or above 21.9 °C for 67 consecutive days [22]. The bimodal distribution of arrival timing for Skaha Lake Okanagan Sockeye (Fig. 6) could prove critical for population viability since a greater proportion of adults arrive prior to the summer thermal barrier.

Recreational, tribal, and commercial harvest opportunities further complicate management of Okanagan

Sockeye during summer months. An average of 19% of Okanagan Sockeye are harvested between Wells Dam (rkm 830) and spawning grounds each year, often when fish are congregated in large numbers at the thermal barrier [37]. Mortality of fish that evade capture compounds this issue: some fishery managers apply a 40–60% mortality rate for salmon released from commercial gillnets and 10% for salmon release from recreational fisheries, rates that increase with increasing water temperatures [57]. A more detailed analysis that accounts for harvest and water temperatures in conversion rates would provide important insights to managers as droughts in the Western United States increase in frequency and duration [30]. Additional research on adult holding and harvest in the Canadian portions of Osoyoos Lake would also provide important insights.

Key differences in physical attributes and post-release performance were observed between Okanagan Sockeye released in Skaha Lake versus those released in Osoyoos Lake. Smolts tagged in Skaha Lake were typically larger (~ 10–20 mm in median total length) and migrated faster, though had lower downstream smolt survival compared to those tagged in Osoyoos Lake. Survival was still lower for smolts tagged in Skaha Lake after adjusting for distance, so some biological or ecological mechanism likely affects smolts derived from hatchery-origin fry introduced into Skaha Lake. Greater rates of predation due to size differences [66], behavioral patterns [58], or migration past a specific location of high predation [25] present possible explanations. Vaseux Lake, located downstream of Skaha Lake, is relatively shallow and hosts large populations of Northern Pikeminnow *Ptychocheilus oregonensis* and Smallmouth Bass *Micropterus dolomieu* that likely influence juvenile survival. Cessation of migration or alternative life history patterns (i.e., non-migrants are perceived as mortality in mark–recapture modeling) once Skaha Lake smolts encounter the productive Osoyoos Lake is another possibility [37]. Finally, differences between hatchery- and wild-origin juvenile Okanagan Sockeye could explain differences in survival during the smolt emigration [35, 56].

Despite lower smolt survival in freshwater, fish originating from Skaha Lake had higher SARs than cohorts tagged in Osoyoos Lake. This may be a result of size or time at ocean entry [18], their differing age structure [54], size-selective harvest [41], or another mechanism that we are unable to account for in these analyses. Adults originating from Skaha Lake had a younger age structure compared to cohorts tagged in Osoyoos Lake, with a significantly greater proportion of jacks (34% versus 18% of adults, respectively). Research has demonstrated how selective pressures can increase and perpetuate the prevalence of jacks, which could be a factor in Skaha Lake [17]. While the younger age structure may increase ocean survival and spawning escapement, the higher proportion of jacks originating from Skaha Lake may translate to reduced reproductive success [10]. Run timing is potentially the most important difference in adult returns of Okanagan Sockeye observed in this study: arrival date to the Okanagan River Basin (OKC site) was earlier and more protracted for Skaha Lake adults with a large pulse arriving in July and then again in late September compared to cohorts tagged in Osoyoos Lake, which arrive in mid–late September. Delays in the spawning migration of Okanagan Sockeye often translate to higher rates of mortality, particularly during higher water temperatures. Adults with a tendency to migrate earlier may fare better in future years by avoiding thermal barriers, greater pre-spawn mortality, or inadvertent mortality related to commercial and recreational fisheries [33, 45]. Conversely, later run timing may translate to avoidance of higher water temperatures in spawning tributaries, a well-documented occurrence in the Fraser River [32]. In either case, maintaining diversity in life history strategies of Okanagan Sockeye will be critical to sustaining the population in a changing climate.

These analyses highlight variability in survival and behavior of Okanagan Sockeye that can inform key aspects of population viability (i.e., VSP) [48]. First, survival during the smolt migration, in the ocean, and during the spawning migration has a profound influence on productivity and, therefore, abundance of Okanagan Sockeye. While ocean survival [69] and increased escapements of Okanagan Sockeye [33, 36] have generally driven productivity and abundance of Columbia River Sockeye Salmon, the 2015 drought clearly illustrates how above-average water temperatures during the spawning migration can negate the production of millions of fish during the last months of life. Second, the increased spatial structure (through reintroduction into historical spawning and rearing locations) and diversity (including migratory timing, smolt size, and adult age structure) highlighted in our analyses demonstrate how management efforts have directly improved biodiversity of Okanagan Sockeye.

The importance of rebuilding diverse wild populations, or functioning portfolios, has been demonstrated in other Sockeye Salmon populations [57]. The findings reported here and impressive recovery of Okanagan Sockeye through the early 2010s demonstrate their resilience to a highly modified environment, whereas the drought in 2015 reminded managers how years of success can be erased by changing river conditions. Routine monitoring to inform management efforts that improve aspects of population viability will be critical in preserving Okanagan Sockeye over the next century. The current monitoring framework and analyses presented here could be improved by (1) additional PIT-tagging and improved detection arrays; (2) more detailed analyses of metrics presented herein; and (3) consideration of additional monitoring tools, such as life cycle modeling [45], that can be used to understand which components of the population warrant the greatest level of protection.

Abbreviations

BO1: Bonneville Bradford Island Ladder; BO2: Bonneville Cascades Island Ladder; BO3: Bonneville Washington Shore Ladder; BO4: Bonneville Washington Ladder slots; MC1: McNary Oregon Shore Ladder; MC2: McNary Washington Shore Ladder; WEA: Wells Dam adult fishways; BON: Bonneville Dam; CJS: Cormack–Jolly–Seber; CRITFC: Columbia River Inter-Tribal Fish Commission; DART: Data Acquisition in Real Time; DFO: Fisheries and Oceans Canada; OKC: Okanagan Channel instream detection site; OKP: Penticton Channel instream detection array; OSOYOL: Osoyoos Lake; OSOYHA: Osoyoos Lake at Haynes Point Campground; OSOYBR: Osoyoos Lake Narrows Highway 3 Bridge; PIT: Passive integrated transponder; PTAGIS: Columbia Basin PIT Tag Information System (www.ptagis.org); SKA: Skaha; SKATAL: Skaha Tailrace; SKAHAL: Skaha Lake; SAR: Smolt-to-adult return; SE: Standard error; VSP: Viable Salmonid Population.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-021-00262-y.

Additional file 1: Appendix S1. Tag Files from PTAGIS of juvenile Sockeye tagged in the Okanagan basin from 2012 to 2019 used in juvenile survival and travel time queries and estimates.

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Authors' contributions

JM led study design, analyses, data interpretation, and technical writing. KH and JF supported technical writing and data interpretation. EK provided statistical support and conducted regression analyses. SF and RB led program development and data collection, also providing support on data interpretation and technical writing. KS performed initial data queries and survival analyses. All authors read and approved the final manuscript.

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Availability of supporting data

The data sets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Data analyzed in this manuscript were obtained under an existing fish tagging program. All tagging followed regionally accepted protocols that minimize stress and injury to PIT-tagged salmonids. The document is available at http://www.biomark.com/Documents%20and%20Settings/67/Site%20Documents/PDFs/Fish%20Tagging%20Methods.pdf

Consent for publication

Not applicable; data are not derived from any individual person.

Competing interests

The authors declare that they have no competing interests.

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