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Estimating predation of adult sockeye salmon by American white pelicans in the Columbia River using a state-space Bayesian approach

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Abstract

Adult sockeye salmon (*Oncorhynchus nerka*) migrate past the largest breeding colony of American white pelicans (*Pelecanus erythrorhynchos)* in the Columbia River, USA. To investigate the magnitude of pelican predation on sockeye salmon, a state-space Bayesian model was used to estimate spatially and temporally explicit predation and survival probabilities, and to estimate the total number of salmon consumed by pelicans each year. Results show that pelican predation was a substantial source of salmon mortality in some years, with median predation probabilities ranging annually from 0.015 to 0.084, resulting in an estimate of 1328 to 47 265 fish consumed annually from 2014 to 2023. While there was evidence that predation probabilities were associated with the number of sockeye salmon returning to the Columbia River annually, there was no evidence that fish length was associated with susceptibility to predation. Additional research aimed at investigating how other biotic and abiotic factors influence sockeye salmon susceptibility to pelican predation are needed to broaden our understanding of predator–prey interactions and to determine to what degree predation limits sockeye salmon survival prior to spawning.

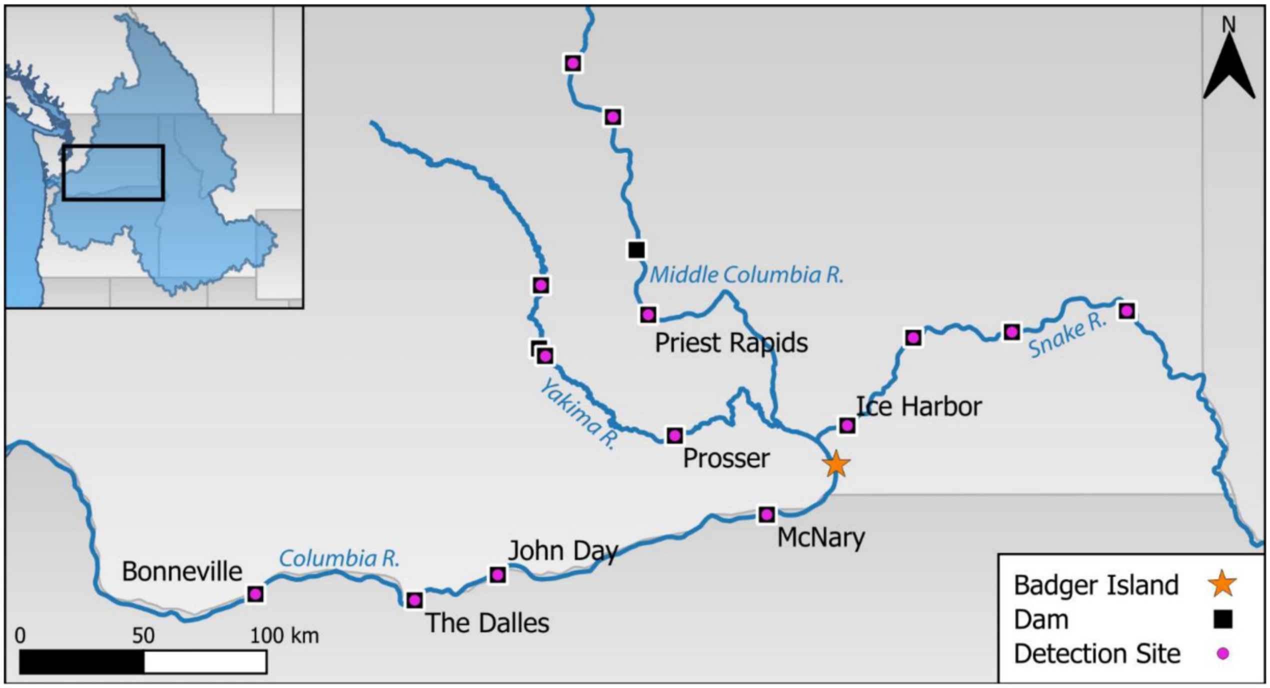
Key words: Bayesian statistics, predator–prey interactions, listed-species, avian predation, sockeye salmon

Introduction

Accurate assessment of cause-specific mortality is critical to understanding factors that affect the survival of salmonids (*Oncorhynchus* spp.) and other animals of conservation concern. Previously published research has indicated that predation by Caspian terns (*Hydroprogne caspia*), double-crested cormorants (*Phalacrocorax auratus*), and several gull species (*Larus* spp.) are substantial sources of mortality to juvenile (smolt) salmonids in the Columbia River, USA (Collis et al. 2001; Antolos et al. 2005; Evans et al. 2012). For instance, Evans et al. (2019) documented predation on Endangered Species Act (ESA) listed Upper Columbia River steelhead (*Oncorhynchus mykiss*) smolts by terns, cormorants, and gulls nesting at up to 14 different breeding colonies, where observed predation probabilities were greater than 0.40 or 40% in some years. American white pelicans (*Pelecanus erythrorhynchos*) also nest on islands in the Columbia River and are indigenous to North America, but few studies have quantified predation effects by pelicans in the Columbia River Basin (CRB; Payton et al. 2023). American white pelicans (hereafter "pelican" or "pelicans") are the largest (by mass, wingspan, and gape) piscivorous colonial waterbird species in North America (Sibley 2014) and unlike most other piscivorous colonial waterbirds, are capable of consuming larger, adult-sized fishes, including adult salmonids and catostomids (Scoppettone et al. 2006; Teuscher et al. 2015; Evans et al. 2016; Budy et al. 2022).

Sockeye salmon (*Oncorhynchus nerka*) are also indigenous to western North America, where they are an integral part of Tribal culture and subsistence for Native Americans in the CRB and are highly valued as a resource for recreational fisheries. Historically, numbers of adult sockeye salmon returning to the CRB were estimated to exceed 2.5 million fish annually (Chapman 1986) but dam proliferation during the early 20th century greatly reduced the species range and abundance (Gustafson et al. 1997). For example, sockeye salmon originating from the Sawtooth Valley of Idaho (Snake River sockeye salmon) were reduced to a single population in Redfish Lake, which became the first fish population to be ESA-listed in the Pacific Northwest (Gustafson et al. 1997; Kozfkay et al. 2019; NMFS 2019). In the Yakima River, WA, construction of high head dams blocked access for sockeye salmon to four nursery lakes, eliminating the species from the basin for nearly 100 years prior to

Fig. 1. Mark–recapture–recovery locations of passive integrated transponder (PIT) tagged sockeye salmon initially detected/released at Bonneville Dam fishways on the Columbia River. Recapture locations include fishways at The Dalles Dam, John Day Dam, and McNary Dam on the Columbia River, Ice Harbor Dam and other dams on the Snake River, Prosser Dam and other dams on the Yakima River, and Priest Rapids Dam and other dams on the middle Columbia River. The recovery location was at the American White Pelican breeding site on Badger Island on the Columbia River. Data used to create this map were extracted from PIT Tag Information Systems, NOAA GeoPlatfrom (https://noaa.hub.arcgis.com/datasets/noaa::columbia-river-basin), and the Natural Earth data (https://www.naturalearthdata.com) in QGIS 3.34 (PSFMC 2023, QGIS Development Team 2024). All projections were in WGS84.



a recent reintroduction effort (Fulton 1970; Matala et al. 2019).

The objectives of this study were aimed at characterizing the impact of pelican predation on regional sockeye salmon populations using the following metrics: (1) estimating the predation probabilities of sockeye salmon by pelicans nesting on Badger Island (BGI), (2) delineating the temporal and spatial extent of pelican predation in the river, (3) estimating the proportion of total sockeye salmon mortality (1–survival) that can be attributed to pelican predation, (4) estimating the total number of sockeye salmon consumed by pelicans, and (5) evaluating the susceptibility of sockeye salmon to pelican predation on the basis of fish size (fork-length). Predation and survival analyses were conducted retrospectively for return years 2014–2023 using mark, recapture, and recovery observations queried from a passive integrated transponder (PIT) tag database (PTAGIS; PSMFC 2024). Collectively, results were used to identify where and when sockeye salmon mortality occurred and the cause of that mortality (BGI pelican predation or unknown mortality). Results provide novel information on pelican predation of adult salmon during freshwater migration over multiple spatial (river-reaches) and temporal (weeks, years) scales during the 10-year study period (2014–2023).

Methods

Mark–recapture–recovery

Predation and total mortality (1–survival) was investigated for sockeye salmon that were captured and PIT-tagged at Bonneville Dam (BON) fishways, or recaptured (i.e., previously PIT-tagged) at those fishways each return year from 2014 through 2023 (Fig. 1). BON, located at river kilometer (rkm) 234 in the Columbia River, is the first dam that sockeye salmon encountered during their spawning migration from the ocean. All sockeye salmon included in this study were captured, handled, and tagged as part of separate, independent studies. Raw data used in this study were acquired from a publicly available database (PSFMC 2024). As such, no additional permits or ethics approvals were necessary to complete this retrospective analysis of data. Each return year, sockeye salmon of unknown origin were captured at the BON Adult Fish Facility. During handling, fish were scanned for an existing PIT-tag. Untagged fish were PIT-tagged (12 × 2 mm, 134 kHz, full-duplex, Biomark, Boise, Idaho) measured for fork-length (mm) and released back into the fishway to resume upstream migration. Passive recapture of adult sockeye salmon occurred via tag detection at PIT-tag antenna arrays (a series of antennas) installed in each BON fishways.

Recaptured sockeye salmon were initially tagged as juveniles 1–3 years prior to returning to BON as adults. Sockeye salmon tagged or recaptured at BON originated from three distinct populations (NMFS 2019) in the Wenatchee River, Okanogan River, Snake River, and Yakima River Basins (Fig. 1). Sockeye salmon have been recently introduced to the Yakima River Basin derived from the Wenatchee River and Okanagan River populations (Matala et al. 2019).

Following detection at BON, PIT-tagged sockeye salmon were subsequently detected passing upstream fishways (and thus assumed to be alive) located at The Dalles Dam (TDA, rkm 311), John Day Dam (JDA, rkm 349), and McNary Dam (MCN, rkm 470) on the Columbia River. Following passage at MCN, sockeye salmon returning to their natal systems on the Snake River (rkm 522), Yakima River (rkm 539), or middle Columbia River (Wenatchee and Okanogan populations) were first detected at Ice Harbor Dam (ICH, rkm 16) on the Snake River, Prosser Dam (PRO, rkm 76) on the Yakima River, or at Priest Rapids Dam (PRD, rkm 639) on the middle Columbia River, respectively (Fig. 1). Fishway detections at each of these dams were used to define river reaches for estimating spatially explicit predation and survival rates. As a tagged fish may migrate past a dam without being detected, several additional PIT tag detection sites and recapture events upstream of ICH, PRO, and PRD (e.g., fishways, instream arrays, and hatcheries) were used to construct encounter histories to estimate detection probabilities of sockeye salmon passing dams within each river reach (Fig. 1). Some PIT tags implanted in sockeye salmon were also recovered (i.e., consumed fish) on the pelican breeding site on BGI (rkm 512) in McNary Reservoir, located upstream of BON but downstream of ICH, PRO, and PRD (Fig. 1). The methods of Evans et al. (2012) were used to recover PIT tags from BGI. In brief, portable PIT tag antennas were used to detect deposited tags after birds dispersed from BGI following the breeding season in late-September or early-October, depending on the year. The entire land area occupied by nesting birds was scanned for tags following each breeding season, with a minimum of two complete sweeps or passes conducted each year. The land area occupied by birds during each breeding season was determined based on georeferenced aerial images of the colony taken during the peak breeding period of late-May to late-June.

Not all PIT tags ingested by pelicans were deposited on the bird's nesting colony (i.e., deposition probabilities were less than 1.0) and not all deposited tags were detected after the breeding season (i.e., detection probabilities were less than 1.0). For instance, some consumed tags were regurgitated or defecated at off-colony loafing or roosting sites, while deposited tags may be removed or damaged by wind or water erosion, or deposited tags may be missed (not detected) during the scanning process (see also Hostetter et al. 2015). Given these known sources of tag loss, an accurate estimate of the total number of tagged sockeye salmon consumed by pelicans required an adjustment or correction for PIT-tag deposition and detection probabilities specific to BGI. The methods and data of Evans et al. (2022*b*) and Payton et al. (2023) were used to estimate deposition and detection probabilities for use in this study. In brief, to estimate detection probabilities, PIT tags with known tag codes were intentionally sown on BGI by researchers prior to and following the breeding season. Recoveries of these tags following the breeding season were then used to infer the probability of detecting tags which were deposited during the breeding season (see survival and predation estimation for additional details). To estimate deposition probabilities, salmonids implanted with PIT tags with known codes were fed to pelicans from BGI during the peak breeding season. The numbers of ingested tags subsequently detected by researchers on BGI following the breeding season were used to estimate deposition probabilities. PIT tag detection and deposition probabilities (collectively referred to as "recovery probabilities") used in this study were those previously published by Evans et al. (2022*a*) and Payton et al. (2023); see also Supplementary materials).

Following detection at PRD, an unknown number of PIT-tagged sockeye salmon were captured and translocated for release into Cle Elum Lake in the Yakima River Basin upstream of PRO as part of a reintroduction program (Matala et al. 2019). As such, accurate estimates of reach-specific survival could not be generated upstream of PRD because an unknown number of tagged fish were removed following passage at PRD (see predation and survival estimation for additional details). Estimates of predation probabilities were, however, generated based on the number of tagged fish that were last seen alive at PRO/PRD/ICH and subsequently recovered on the BGI pelican breeding site.

Predation and survival estimation

The joint mortality and survival (JMS) estimation methods of Payton et al. (2019) were used to estimate reach-specific and cumulative sockeye salmon predation and survival probabilities. This hierarchical state-space Bayesian model incorporated detections of both live and dead PIT-tagged sockeye salmon in space and time to simultaneously estimate predation and survival. Temporal variation both within and across years was assumed to be inherent to rates of mortality (Evans et al. 2014; Hostetter et al. 2015), recapture (Sandford and Smith 2002), and recovery (Ryan et al. 2003; Evans et al. 2012). Therefore, cohorts (groups of fish that were assumed to have experienced similar rates of mortality/survival and recapture) were defined by year and week of passage at BON. Here, data, parameters, and likelihood equations of the employed model for all PIT-tagged sockeye salmon released in each cohort are described. Subsequently, the modelling of variation in these probabilities across time is detailed.

The primary data informing the model consisted of two vectors, y and r, describing each fish's recapture (passive encounter) and tag recovery history. The vector y is a J-length vector, where y_j is an indicator variable of the successful recapture of the fish at recapture opportunity j, delineating the end of segment j for $j = \{1, 2, \ldots, J - 1\}$ and $j = J$ representing the upper-bound of the pertinent study area. For the years 2014–2016, $J = 3$ represents the river segments from BON to TDA, TDA to MCN, MCN to PRO/PRD/ICH, and the entire river extent upstream of PRO/PRD/ICH. Following the installation of PIT-tag arrays in the adult ladders at John Day Dam in 2017, the study considered $J = 4$ river segments with the

TDA to MCN segment split into TDA to JDA and JDA to MCN. The vector r is a 2-length single-entry unit vector identifying each fish's recovery or lack thereof where $r_1 = 1$ indicated recovery from the pelican colony and $r_2 = 1$ indicated a non-recovery.

Two parameters were of primary importance in defining the model:

p is a J-length vector, where p_j represents the probability that a fish alive at recapture opportunity j was successfully recaptured for $j = \{1, 2,\ldots, J\text{-}1\}$ and $p_J = 1$ represented the assumed perfect detection of fish leaving the upper-bound of the pertinent study area. θ is a J $\times$ 2 matrix, where $\theta_{j,d}$ represents the probability (from release) that a fish entered segment j alive and then, prior to exiting segment j, subsequently succumbed to predation by pelicans on BGI for $d = 1$ or from some unspecified cause of mortality (including natural causes following spawning) for $d = 2$. Implicit from this parameterization is that survival from release through some given segment k is equal to $1 - \sum_{d<k} \sum_{d} \Theta_{j,d}$

An additional parameter vector was needed to enumerate the likelihood of recovering tags:

γ, a 2-length vector where γ_1 represented the probability of recovering a fish which died due to depredation by pelicans nesting on BGI, and $\gamma_2 = 0$ represented the lack of recoveries of fish which died from all other unspecified causes. The parameter γ_1 represents the probability of a consumed tag being deposited and redetected by researchers following the breeding season.

The employed model can be expressed by incorporating these parameters into recursive functions, $\chi_{j,d}$, which are defined to represent the probability for the recovery of a fish that was not subsequently recaptured after entering segment j given its subsequent recovery or lack thereof. The probability of a tag being recovered from the pelican colony on BGI can be expressed as

$$\chi_{j,1} = \theta_{j,1} * \gamma_1 + \left(1 - p_j\right) * \chi_{j+1,1}$$

and the probability of a tag being unrecovered can be expressed as

$$\chi_{j,2} = \theta_{j,1} * (1 - \gamma_1) + \theta_{j,2} + \left(1 - p_j\right) * \chi_{j+1,2}.$$

There were considerable differences in how the probabilities of mortality, recapture, and recovery were related among the temporal cohorts. Probabilities of the recovery of consumed tags (deposition and detection combined) were assumed to be equal among sockeye salmon populations and within each day of release. As described above, informed priors were employed to estimate probabilities of deposition and detection of deposited tags, which explicitly accounts for the increasing likelihood of detecting tags that were deposited later in the year. Probabilities of recapture were assumed to be independent from year to year. Within a given year the log-odds of recapture at a given recapture opportunity site on a given day were assumed to be equal to the log-odds for the previous day plus (or minus) some random error

$$\log\left(\frac{p_{i+1}}{1 - p_{i+1}}\right) = \log\left(\frac{p_i}{1 - p_i}\right) + \epsilon_i$$

where i denotes the daily cohort, where $\epsilon_i \sim$ Normal $(0, \sigma_\epsilon)$ $\forall\, i$ and the prior distribution for the probability of recapture on the first day was assumed to be Uniform(0,1). Aggregate survival/mortality probabilities were also assumed to be independent from year to year. Similar to the modelling of recapture probabilities, serial correlation among days was accounted for with a log-odds random-walk approach, as described by Payton et al. (2019). Additionally, the informed partitioning methods of Evans et al. (2022*b*) were used to allow for the sharing of information among years to increase the precision of reach-specific estimates. In brief, a vector of aggregate life path possibilities was constructed, including cumulative probability (across all segments) of predation and segment-specific probabilities of mortality from unspecified sources, to be the basis for modelling variations across days. The cumulative probability of predation was subsequently partitioned across river segments. For a given year, the log-odds of each aggregate life path possibility on a given day were assumed to be equal to the respective log-odds in the previous day plus (or minus) some random error

$$\log\left(\frac{\overset{\rightharpoonup}{\theta}{}^{*}_{i+1}}{\theta^{*}_{ref,i+1}}\right) = \log\left(\frac{\overset{\rightharpoonup}{\theta}{}^{*}_{i}}{\theta^{*}_{ref,i}}\right) + \epsilon_i$$

where $\overset{\rightharpoonup}{\theta}{}^{*} = vec\,(\theta)$ (i.e., a vectorization of θ), with θ^{*}_{ref} ref denoting the reference level, defined to be death from an unspecified source in the final segment; i denotes the daily cohort; and $\delta_{ji} \sim$ Normal $(0, \sigma_\delta)$ $\forall\, i$. We refer readers to Payton et al. (2019) for more details. Each vector representing the probabilities for the aggregated life path possibilities is a simplex, and the prior distribution for the initial day's simplex was assumed to be Dirichlet(1), where 1 is an appropriately sized vector of ones. Weakly informative priors of HalfNormal(1) were also implemented for all random-walk variance parameters. Previous testing and applications of the JMS model have demonstrated that given sufficient data, the information provided by prior distribution assignments has negligible impacts on predation and survival estimates but is valuable for computational efficiency. Annual estimates were calculated as weighted averages, defined by weekly release counts within each biological cohort.

All models were implemented with the software Stan accessed through R version 4.3.2 (R Core Team 2023) using RStan version 2.32.5 (Stan Development Team 2023). To simulate random draws from the joint posterior distribution, four Hamiltonian Monte Carlo–Markov chain processes were run. Each chain contained 4000 adaptation iterations, followed by 4000 posterior iterations. Posterior iterations were then thinned by a factor of 4. Chain convergence was visually evaluated and verified using the Gelman–Rubin statistic (Gelman et al. 2013), and all accepted chains reported zero divergent transitions. All estimates represent posterior distribution medians, with 95% credible intervals (CRIs)

Table 1. Numbers of passive integrated transponder (PIT) tagged sockeye salmon detected/released at Bonneville Dam (BON) that were subsequently detected alive passing upstream dams or recovered dead (in parentheses) at the American white pelican colony on Badger Island after passage at each dam.

		Columbia River			Yakima River	Mid-Columbia River	Snake River
Year	BON	TDA	JDA	MCN	PRO	PRD	ICH
2014	2461 (0)	2163 (3)	NA	1900 (5)	3 (0)	1685 (7)	198 (1)
2015	2009(0)	1559 (23)	NA	1073 (16)	2 (0)	771 (2)	64 (5)
2016	1986 (0)	1801 (7)	NA	1631 (5)	24 (0)	1466 (3)	125 (0)
2017	1283 (0)	1101 (0)	1024 (7)	950 (4)	7 (0)	862 (1)	45 (1)
2018	1959 (0)	1783 (0)	1679 (2)	1632 (6)	6 (0)	1594 (0)	9 (0)
2019	1005 (0)	922 (1)	872 (3)	838 (0)	5 (1)	778 (0)	6 (0)
2020	2092 (1)	1898 (3)	1781 (6)	1751 (6)	14 (0)	1656 (1)	9 (0)
2021	1913 (1)	1584 (2)	1446 (33)	1242 (15)	0	1054 (2)	30 (1)
2022	1916 (0)	1738 (7)	1670 (5)	1586 (6)	0	1440 (1)	94(1)
2023	1829 (0)	1612 (4)	1468 (21)	1233 (27)	0	1010 (3)	77 (2)
All	18 453 (2)	16 161 (50)	9940 (77)	13 836 (90)	61 (1)	12 316 (20)	657 (11)

Note: PIT tag arrays were located in fishways at BON, the Dalles Dam (TDA), John Day Dam (JDA; staring in 2017), and McNary Dam (MCN) on the Columbia River; at Prosser Dam (PRO) on the Yakima River; at Priest Rapids Dam (PRD) on the middle Columbia River; and at Ice Harbor Dam (ICH) on the Snake River. See Fig. 1 for a map of mark, recapture, and recovery locations.

representing the highest density intervals calculated with HD Interval version 0.2 (Meredith and Kruschke 2022).

Consumption estimation

Estimates of weekly predation probabilities generated from the JMS model, coupled with information on the total number of adult sockeye salmon (tagged and untagged) counted at BON fishways each week, were used to estimate the total number of sockeye salmon consumed by BGI pelicans. Data on the number of sockeye salmon passing BON fishways was obtained from fishway or ladder counts (FPC 2023). Data were derived from observed counts of sockeye salmon passing through ladder viewing windows 50 min out of every hour from 0400 to 2000 Pacific Standard Time. Observers count for 50 min of each hour and the resulting counts were then multiplied by 1.2 to get a total daytime count. Video surveillance was used from 2000 to 0400 PST, with video counts added into the daytime count. Detailed counting metadata from fishways at BON are available from the Fish Passage Center (FPC 2023). Counts were summed by week and year (2014–2023). The simulated draws from the joint survival and predation posterior distribution associated with weekly predation probabilities were then multiplied by the observed number of fish counted at BON to obtain estimates of consumption. Estimates of uncertainty were not available for weekly fishway counts. Technician counting personnel, however, were subject to a 1 h test each month with a supervising counter and counts between both observers (technician and supervisor) were found to be within 95% per salmonid species, per test, suggesting counts were precise (see also FPC 2023).

Size selectivity

To evaluate the relationship between fish size (fork-length, mm) and susceptibility to pelican predation, the size distribution of sockeye salmon tagged at BON was compared with the size distribution of sockeye salmon subsequently consumed by pelicans breeding on BGI. Distributions were plotted as the proportion or density of fish by length from each sample (at BON and BGI) and Kolmogorov–Smirnov tests (D) were used to investigate if the difference was statistically significant.

Results

Mark–recapture–recovery

Recapture and recovery probabilities were generated to be employed in the JMS models to estimate predation and survival. In total, 18 453 sockeye salmon were available for use in the study (Table 1). Of these, 14 049 were PIT-tagged (marked) at BON and 4404 were recaptured (i.e., previously tagged) at BON during 2014–2023. Sample sizes of PIT-tagged sockeye salmon varied by year, ranging annually from 1005 in 2019 to 2460 in 2014 (Table 1). The proportion of tagged sockeye salmon at BON that were subsequently detected passing upstream dams also varied by year and dam, but decreased as fish migrated upstream and as fish entered the Yakima River, middle Columbia River, and Snake River after passing McNary Dam on the Columbia River (Table 1). In total, 251 tags were recovered on the BGI pelican colony, ranging from 5 to 57 tags annually (Table 1). Of these, 191 and 60 were from fish tagged at or recaptured at BON, respectively. The number of recaptured or recovered tags does not account for recapture probabilities at each upstream dam or recovery probabilities on the BGI pelican colony and thus represent minimum numbers of surviving and depredated fish each year (see Methods). Recapture probabilities of tagged fish at fishways were high, ranging annually from 0.95 (95% CRI = 0.94–0.96) to 1.0, indicating the vast majority of sockeye salmon were detected in fishways located at each dam within the study area. Recovery probabilities of tags on the BGI pelican colony ranged annually from 0.24 (0.16–0.33) to 0.37 (0.19–0.53), indicating that the majority of tags consumed (via sockeye salmon predation) by pelicans were not detected on BGI following each breeding season. Recapture and recovery probabilities used to generate estimates of predation and survival are provided in Supplementary materials, Table S1.

Predation and survival

Results from our JMS models indicated that BGI pelican predation was a substantial source of sockeye salmon mortality in some, but not all, study years. Estimated predation probabilities of PIT-tagged sockeye salmon during passage through Reach 1 (BON to TDA) ranged annually from <0.001 (the lowest reportable estimate) to 0.002 (95% CRI = 0.001–0.008) of available fish, indicating that a small proportion of sockeye salmon were consumed by BGI pelicans in the first river reach evaluated (Fig. 2). Estimated predation probabilities in Reach 2 (TDA to JDA) were slightly higher than those of Reach 1, ranging annually from <0.001 to 0.005 (0.001–0.013) of available sockeye salmon (Fig. 2). Estimated predation probabilities in Reach 3 (JDA to MCN) were consistently higher than those of Reach 1 and 2, ranging annually from 0.002 (0.001–0.007) to 0.059 (0.037–0.084; Fig. 2). During 2014–2016 estimates were measured across both Reach 2 and Reach 3 combined (TDA to MCN) due to a lack of PIT-tag detection capabilities at JDA in those years. Estimates from TDA to MCN ranged annually from 0.004 (0.001–0.010) to 0.048 (0.025–0.070; Fig. 2), significantly higher than those observed in Reaches 1 and 2. Estimated predation probabilities in Reach 4 (MCN to PRO/PRD/ICH), the furthest upstream reach evaluated, ranged annually from 0.001 (<0.001–0.006) to 0.061 (0.033–0.102; Fig. 2). Predation was also documented upstream of PRO/PRD/ICH, with fish last detected at all three dams being consumed by BGI pelicans (Table 1). The potential collection and subsequent transport of tagged sockeye salmon from PRD to upstream of PRO (Matala et al. 2019), however, precluded estimates of survival probabilities in reaches upstream of PRD (see Methods). Nonetheless, there was evidence that pelican predation occurred upstream of PRO, PRD, and ICH (Table 1) with an estimated <0.001 to 0.035 (0.017–0.061) of sockeye salmon consumed annually by BGI pelicans during the study. Results indicated that pelicans breeding on BGI were commuting a minimum of 200 rkm downstream of TDA and a minimum of 127 rkm upstream of PRD to forage on sockeye salmon in some years. Most of the predation, however, occurred in the two river reaches (Reaches 3 and 4) in closest proximity to BGI (Figs. 1 and 2).

Estimated total or aggregate predation probabilities (predation across all river-reaches upstream of BON) ranged annually from 0.015 (0.007–0.024) in 2019 to 0.084 (0.056–0.116) in 2015 (Table 2). Estimates of total predation incorporate all tags recovered on the BGI pelican colony, regardless of the river reach in which predation occurred and was based on the number of sockeye salmon initially tagged at or recaptured at BON.

Analogous to estimates of predation, estimates of reach-specific total mortality (1–survival) also varied considerably by river reach and year, ranging annually from 0.018 (0.001–0.057) to 0.217 (0.202–0.234) per reach, per year (Fig. 2). In most years, total mortality was highest in Reach 1, with estimates greater than 0.080 observed in all study years (Fig. 2). In 2015 and 2021, however, mortality was significantly higher upstream of TDA in Reaches 2 and 3, with an estimated 0.153 (0.135–0.171) mortality rate observed between JDA and MCN in 2021 and 0.373 (0.351–0.393) mortality rate between TDA and MCN (Reach 2 and 3 combined) in 2015 (Fig. 2). Comparisons of reach-specific total mortality and mortality due to pelican predation (depicted as a percentage) indicated that pelicans accounted for <1% of all sockeye salmon mortality sources during passage through Reach 1 but up to 44.7% (23.3%–70.2%) of all mortality sources during passage through Reach 3 in some years (Fig. 2). The relative effects of pelican predation were consistently the greatest during sockeye salmon passage through reaches 3 and 4, the reaches closest to BGI. Comparisons of total mortality and mortality due to BGI pelican predation during passage through the entire study area ranged annually from 5.5% (2.5%–9.2%) to 18.5% (12.8%–24.8%).

Consumption

Pelican predation of sockeye salmon was documented throughout the migration period in each study year. The total number of sockeye salmon counted in fishways at BON (total Columbia River escapement) was highly variable within (weekly) and across (annual) study years, ranging annually from 62 828 fish in 2019 to 663 077 fish in 2022 (Table 2). Peak passage was observed between late June to early July (weeks 26–28), but fish were migrating past BON from late May to early September (weeks 20–32) in most years (Fig. 3). Extrapolation of predation probabilities on PIT-tagged sockeye salmon observed at BON to all sockeye salmon (tagged and untagged) counted at BON indicated that pelicans breeding on BGI consumed between 1328 (479–2588) fish and 47 265 (29 747–64 857) fish in 2019 and 2015, respectively (Table 2). Average annual predation and consumption estimates were 0.046 (0.037–0.057) and 13 863 fish (10 891–17 557) respectively, across the study period (2014–2023; Table 2).

Weekly estimates of consumption indicated that sockeye salmon detected passing BON were susceptible to pelican predation throughout the migration period (late May to early September). Results suggest that increases in the number of sockeye salmon passing BON coincided with increases in the number of sockeye salmon consumed by pelicans breeding on BGI (Fig. 3). As such, the majority of sockeye salmon consumed by pelicans were consumed during the peak passage period of late June to early July based on detection dates at BON, with substantially smaller numbers in other time periods in most years (Fig. 3). An exception was predation in 2015 and 2021, where sockeye salmon detected passing BON in late-July and early-August were disproportionately consumed relative to sockeye salmon passing during the peak. Small weekly sample sizes of PIT-tagged sockeye salmon at BON, resulted in imprecise estimates of total consumption, particularly in years with the largest runs, like in 2015.

Size selectivity

Sockeye salmon of all fork-lengths and ages were equally susceptible to pelican predation during the study period. Sockeye salmon tagged at BON ranged in size from 280 to

Fig. 2. Estimated annual reach-specific total mortality (green bars) and mortality from American white pelicans breeding on Badger Island (purple bars) on sockeye salmon during upstream migration from Bonneville Dam (BON) to The Dalles Dam (TDA), TDA to John Day Dam (JDA), JDA to McNary Dam (MCN), MCN to Priest Rapids Dam (PRD) or Prosser Dam (PRO), or Ice Harbor Dam (ICH), and upstream of PRD/PRO/ICH (predation only) during 2014–2023. Error bars depict 95% credible intervals. See Fig. 1 for a map of the study area.

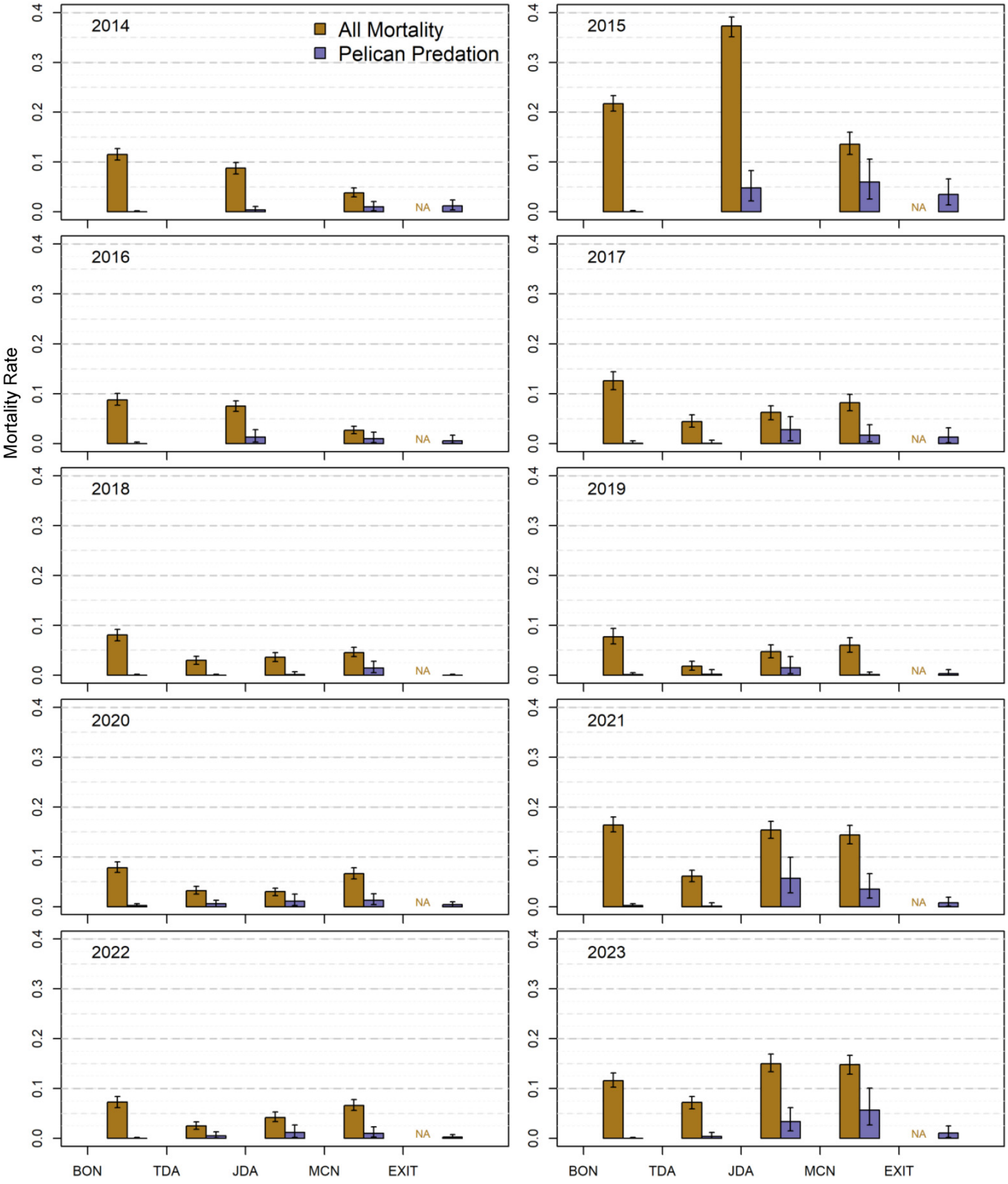


Table 2. Numbers of sockeye salmon with passive integrated transponder (PIT) tags and all fish counted (tagged and untagged) in fishways at Bonneville Dam (BON) during 2014–2023.

Year	No. tagged	Predation probability	No. counted	Estimated consumption
2014	2461	0.022 (0.013–0.032)	614 052	13 483 (7558–19 957)
2015	2009	0.084 (0.056–0.116)	510 497	47 265 (29 747–64 857)
2016	1986	0.027 (0.015–0.044)	342 446	9363 (4924–14 945)
2017	1283	0.049 (0.023–0.075)	87 582	3277 (1699–5497)
2018	1959	0.015 (0.007–0.024)	193 407	2884 (1289–4747)
2019	1005	0.022 (0.007–0.045)	62 828	1328 (479–2588)
2020	2092	0.035 (0.018–0.051)	341 702	9060 (5068–14 165)
2021	1913	0.080 (0.054–0.106)	151 631	12 425 (8153–16 812)
2022	1916	0.026 (0.014–0.043)	663 077	10296 (5393–17 189)
2023	1829	0.083 (0.058–0.109)	565 729	23 951 (16 398–32 052)
Average	1845	0.046 (0.037–0.057)	353,295	13 863 (10 891–17 577)

Note: Average annual predation probabilities (95% credible intervals) by American white pelicans breeding on Badger Island were based on tagged sockeye salmon, estimates that were then extrapolated to all sockeye salmon passing BON (see Methods).

615 mm (Fig. 4). Fish less than 420 mm were likely 3-year-old fish (that matured after 1 year in the ocean), while fish between 420 and 615 mm were a mixture 4- and 5-year-old fish (that matured after 2–3 years in the ocean). It should be noted that the vast majority of 3-year-old fish were of Okanagan origin. The Kolmogorov–Smirnov tests indicated that there was no statistically significant difference in the size distribution of sockeye salmon PIT-tagged at BON compared with those consumed by pelicans breeding on BGI ($D = 0.037$, p-value $= 0.992$).

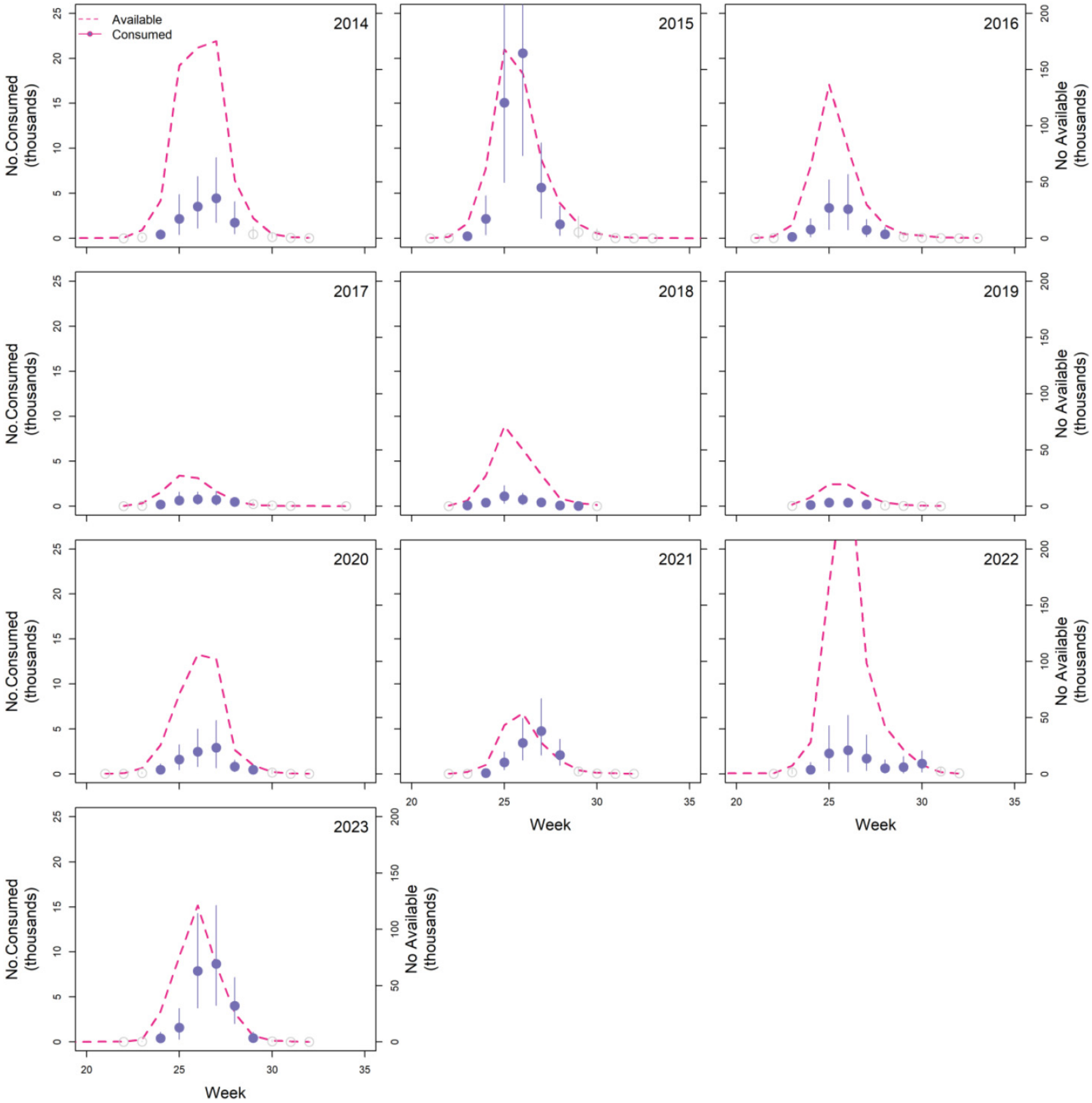
Discussion

Determining cause-specific sources of mortality in adult salmon during freshwater migration is critical for maintaining and protecting fish populations, especially when considering populations of conservation concern. While some improvements have been made to ameliorate the negative effects of dams on fish passage (e.g., installation of fish ladders, flow regulation, and other improvements), our results provide evidence that American white pelicans were a substantial source of adult sockeye salmon mortality in the Columbia River in some years during our study. While previously published studies have documented predation by pelicans on juvenile salmon in the Columbia River (Evans et al. 2012; Payton et al. 2023) and predation by pelicans on resident fish populations elsewhere in North America (Teuscher et al. 2015; Evans et al. 2016; Budy et al. 2022), results from this study provided evidence that pelicans breeding on BGI in the Columbia River consumed a substantial proportion and number of migrating adult salmon, with estimated predation probabilities exceeding 0.08 or 8% and consumption estimates of more than 40 000 fish in some years. Avian predation on adult salmon has the potential to more negatively impact population productivity compared to predation on juvenile salmon. A year class of emigrating juveniles is far more abundant than a cohort of returning adult fish, and adult salmon are much more likely to complete the life cycle and contribute to future recruitment (Quinn 2007). For instance, smolt-to-adult survival rates of ESA-listed Snake River sockeye salmon from Lower Granite Dam on the Snake River (as smolts) to BON on the Columbia River (as adults) averaged 0.008 annually during 2008–2016 (Evans et al. 2022*b*). Given this smolt-to-adult return rate (0.008), pelican predation on a single Snake River sockeye salmon adult would be equivalent to predation of 125 Snake River sockeye salmon smolts.

Previously published studies of avian predation in the CRB have focused on predation probabilities (colloquially “rates”) and not the total number of fish consumed by birds because information on the total number of fish available as prey were not available in these studies (Collis et al. 2001; Antolos et al. 2005; Hostetter et al. 2015; Evans et al. 2022*b*). Counts of the total or absolute number of adult sockeye salmon (tagged and untagged) passing BON, however, provided a way to estimate how many sockeye salmon were consumed by pelicans. Estimates of total consumption incorporated weekly changes in the abundance of sockeye salmon passing BON, providing information on intraannual trends in predation and the magnitude of predation relative to the sockeye salmon run-at-large. Over the span of this study, the number of adult sockeye salmon counted passing BON varied annually by a factor of 10, which resulted in highly variable estimates of consumption, even in cases where estimates of predation probabilities were similar amongst years. For instance, the number of PIT-tagged fish and estimates of predation probabilities were very similar in 2015 and 2021, but estimates of consumption were 47 265 fish and 12 425 fish, respectively, because the sockeye salmon run was 3.4 times larger in 2015 compared with 2021.

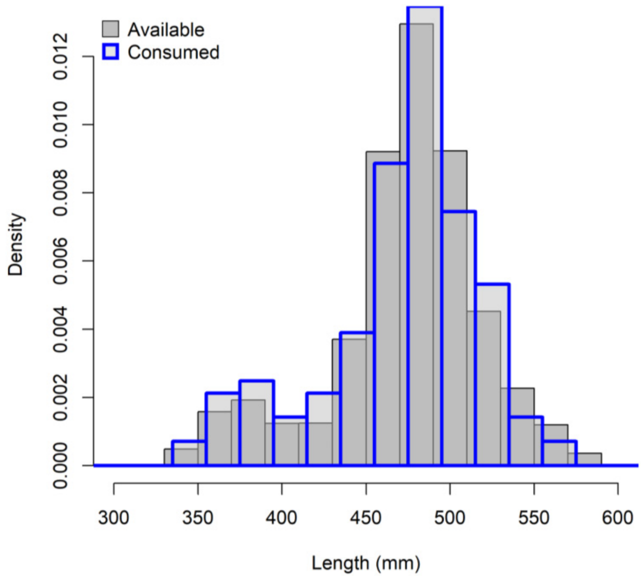
Multiple factors may be associated with the high variation observed in weekly and annual estimates of pelican predation on sockeye salmon, including changes in the abundance or size of the sockeye salmon run, the size of the BGI pelican colony, as well as other biotic and abiotic factors that could influence sockeye salmon susceptibility to pelican predation. From these results, there was some evidence that variation in weekly estimates of predation were associated with

Fig. 3. Number of sockeye salmon counted passing Bonneville Dam and weekly estimates of the number subsequently consumed by American white pelicans breeding on Badger Island during 2014–2023. Error bars depict 95% credible intervals. Open circles represent weeks with less than 100 tagged sockeye salmon available.



the number of sockeye salmon counted passing BON, with increases in predation coincident with increases in sockeye salmon abundance. This pattern suggests a Type II functional response, where the number of prey consumed increases with increasing prey availability or density (Solomon 1949; Yang et al. 2008). This functional response can have highly negative effects on the stability of prey populations at low or declining abundances, which could make species of conservation concern, such as Snake River sockeye salmon, increasingly vulnerable (Solomon 1949). Type II functional responses have been documented at other large (thousands of individuals) piscivorous waterbird colonies in the CRB, but accurate information on the number of predators is necessary to mathematically describe these relationships (Hostetter et al. 2022). Estimates of the peak (maximum) number of adult pelicans counted on BGI during the breeding season were available from other studies and indicated the colony has increased in size since surveys commenced in 2008 (Adkins et al. 2014) and that the years with largest numbers of pelicans on BGI (3267 adults in 2015, 3620 adults in 2021; B. Cramer et al. unpublished report, 2021; Payton et al. 2023) were also the years with the highest estimates of predation in this study. As noted by Hostetter et al. (2022), however, weekly estimates of the number of pelicans breeding

Fig. 4. Length distributions (density of fish as a proportion) of available sockeye salmon PIT-tagged at Bonneville Dam compared with those subsequently consumed by American white pelicans breeding on Badger Island.



on BGI would be necessary to mathematically describe the relationship between colony size and pelican predation impacts within and across years but this information has not been documented.

Several studies have documented that fish length was associated with susceptibility to predation by piscivorous colonial waterbirds in the CRB and elsewhere in North America (Hostetter et al. 2023). In the present study, however, there was no evidence that pelicans were disproportionately consuming adult sockeye salmon based on their length, with larger- and smaller-sized sockeye salmon equally susceptible to pelican predation. Evans et al. (2016) documented that adult lost river suckers (*Deltistes luxatus*) as large as 730 mm were consumed by pelicans breeding on islands in Upper Klamath Lake, or with all but the largest suckers susceptible to pelican predation. Similarly, Scoppettone et al. (2006) confirmed Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*) as large as 700 mm in diets of pelicans breeding on an island in Pyramid Lake, NV. Teuscher et al. (2015) found that pelicans nesting on islands in Blackfoot Reservoir, ID, failed to exhibit size selectivity for Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) with fish up to 600 mm (the largest available) consumed, which is consistent with results of this study. Collectively, these results indicate that pelicans can consume fish greater than 700 mm, and fishes of any species that do not exceed this threshold may be equally susceptible to pelican predation.

Abiotic factors or environmental conditions experienced by adult sockeye salmon during freshwater migration may also be related to pelican predation. For instance, predation effects on sockeye salmon in 2015 and 2021 were amongst the highest observed during the study, especially predation on late-migrating sockeye salmon in July and August. Adult sockeye salmon mortality resulting from increased water temperature during migration has been well documented (Keefer et al. 2008; Martins et al. 2011; Jeffries et al. 2012; Martins et al. 2012; Barnett et al. 2020) and is believed to have resulted in abnormally high mortality for adult sockeye salmon returning to the CRB in 2015 and 2021 (Kozfkay et al. 2017; NOAA 2022). During these years, river temperatures regularly exceeded 20 °C and were as high as 22 °C on some days (CBR 2023).Keefer et al. (2008) found that water temperatures in the 21–24 °C range were strongly associated with increased mortality and decreased travel rates for Snake River sockeye salmon. Hostetter et al. (2023) found that fish travel time and water transit time were inversely related to avian predation susceptibility as slower moving prey experienced temporal increases in exposure to avian predators. Thus, environmental conditions (increased water temperature, decreased river flow) and physiological responses by adult sockeye salmon (such as lethargy and disorientation) were potentially associated with higher pelican predation probabilities in 2015 and 2021. Additionally, an unknown proportion of sockeye salmon consumed by pelicans could have been dead or moribund or otherwise compromised at the time of consumption, especially in years with poor water quality conditions, like in 2015 and 2021. While these appear to be to causal mechanisms, this model was unable to specifically evaluate these factors due to limitations that included small sample sizes of PIT-tagged sockeye salmon (resulting in imprecise estimates of weekly predation probabilities and consumption) and uncertainty regarding environmental conditions that fish experienced during migration prior to being consumed.

Estimates of pelican predation on adult sockeye salmon presented herein represent minimum estimates of predation by all piscivorous waterbirds in the CRB. For instance, small numbers of PIT-tags from adult sockeye salmon tagged or recaptured at BON were recovered on a double-crested cormorant colony ($n = 2$) that was within foraging distance of the study area (PSMFC 2024). Double-crested cormorants have been documented to consume fish upwards of 450 mm (Hatch and Weseloh 1999), so smaller-sized adult sockeye salmon are susceptible to cormorant predation. Adult sockeye salmon, however, likely exceed the gape width of most other piscivorous colonial waterbird species in the CRB, like Caspian terns, gulls, grebes (*Aechmophorus spp.*), and common mergansers (*Mergus merganser*) based on maximum lengths of fish ~350 mm confirmed in the diets of these species (Wiese et al. 2008; Hostetter et al. 2023). Predation of adult sockeye salmon by other pelicans (i.e., those that were not actively breeding on BGI) also likely occurred. For example, predation by pelicans that were sexually immature (non-nesting), failed nesters (unsuccessful), or that dispersed from BGI following the breeding season (but remained in the region to forage) could not be quantified in our study because PIT tag deposition would have occurred at sites other than BGI. Research aimed at quantifying the distribution and foraging behavior of non-breeding, failed breeding, and post-breeding pelicans may therefore be necessary to more fully understand the impacts of pelican predation on sockeye salmon and other fishes of conservation concern in the CRB. Finally, pelicans scoop prey using a large, hooked bill and not all foraging attempts are successful (Knopf and Evans 2004), with some unknown proportion of sockeye salmon injured during foraging attempts; this could result in latent mortality or crippling losses (Reimchen 1988; Payton et al. 2020). The effects of latent mortality on sockeye salmon associated with pelican foraging in the current study, however, was unknown but could be substantial given injuries (predator scars) observed among sockeye salmon in the Yakima River (Kock et al. 2021) and the possibility that these injuries could increase the likelihood of developing fungal or bacterial infections or other anomalies that ultimately lead to failed spawning or death.

Comparisons of all sources of sockeye salmon mortality (1–survival) to mortality due to BGI pelicans indicated that pelican predation accounted for up to 45% of all mortality sources in some river reaches and years, but no more than 19% across all river reaches and years. BGI pelicans were documented consuming sockeye salmon outside (upstream) of the study area but estimates of predation probabilities were low in most years. As such, and assuming predation by non-breeding, failed breeding, and post-breeding pelicans was also relatively low, factors other than BGI pelican predation were the greatest cause(s) of sockeye salmon mortality within the study area. For instance, in Reach 1 (BON to The Dalles Dam), where predation by BGI pelicans was <0.003 in all years, estimates of total mortality were amongst the highest observed at >0.080 in all study years. Potential non-avian sources of mortality in this and other river reaches evaluated include harvest associated with tribal ceremonial, subsistence, and commercial fishing, non-tribal recreational fishing, and a myriad of other factors which have been documented from studies throughout western North America (Quinn et al. 1997; Jeffries et al. 2011; Hinch et al. 2012; Hinch et al. 2021).

Although the results of this study provide evidence that pelicans consume a substantial proportion and number of adult sockeye salmon in some years, the degree to which pelican predation limited the number of sockeye salmon that would have successfully spawned each year in the absence of pelican predation (i.e., the additive effects of pelican predation) are unknown, particularly in years when poor environmental conditions may be the leading cause of sockeye salmon mortality. Given that pelican predation was evident for adult (mature) sockeye salmon of all lengths and that predation occurred throughout the migration period of May–September in all study years, predation on adult sockeye salmon is much more likely to negatively influence population viability than predation on juvenile sockeye salmon. American white pelicans are currently listed as a Species of Greatest Conservation Need in Washington State, where the BGI pelican colony is located (WDFW 2024). Pelicans are also protected by the U.S. Migratory Bird Treaty Act (1918), which prohibits management actions that compromise the conservation status of pelicans. The conservation status of pelicans, along with the endangered status of Snake River sockeye salmon and the ceremonial, subsistence, and recreational value of all sockeye salmon populations in the CRB, could result in conflicts amongst managers that are trying to protect these two native species. Additional research aimed at further investigating how biotic and abiotic factors experienced by sockeye salmon influence their susceptibility to pelican predation may provide management-relevant information and insight to better understand predator–prey interactions that affect fish species of conservation concern.

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Data availability

Data used for this study is publicly available from the PTAGIS, DART, and COE Adult Fish Count online databases (PSFMC 2024, CRB 2024, FPC 2024). Code and data available on Dryad Digital Repository at https://doi.org/10.5061/dryad.3bk3j9kvt.

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Competing interests

The authors declare there are no competing interests. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2024-0270.

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