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Using repeat injury assessments in adult sockeye salmon (*Oncorhynchus nerka*) to predict spawning success and describe severity of migration conditions

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ABSTRACT

Pacific salmon (Oncorhynchus spp.) are semelparous and anadromous, and during their up-river migration to spawn can experience injuries and mortality from fisheries interactions and adverse environmental conditions. There is the potential to improve models used to predict those losses by including information on surficial fish condition, but for this information to be useful, we need to understand how injuries change over time, and how injury type influences this change. To do this, we used repeated individual assessments to examine whether injuries accrued during migration on Fraser River sockeye salmon (O. nerka), assessed in the last leg of their migration or on arrival at the spawning grounds, could be used to predict their final injury score at death after spawning. We found that injury scores increased over the spawning period, but this was not driven by any specific type of migration-related injury, and fish initially scored as 'uninjured' had the largest increase in injury score, indicating a ceiling effect to our scoring method. Females with higher migration-related injury scores were more likely to experience pre-spawn mortality. Initial injury score accrued during migration was positively correlated with final injury score after spawning but only when initially assessed 45 km from the spawning grounds, and females that spawned accrued more injuries than females that did not spawn. Thus our method was able to use pre-spawn injury scores to predict spawning success but was limited in its ability to use post-spawn injury scores to describe severity of migration conditions. This highlights the need to better understand injury and disease dynamics and further refine injury assessment and scoring methods at the individual level if information on surficial fish condition is to be used to either describe or predict migration severity or pre-spawn mortality at the population level.

1. Introduction

Anadromous Pacific salmonids (*Oncorhynchus* spp.) support some of the most intensively studied and managed fisheries in the world as the fish and fisheries are culturally, ecologically, and economically important. There is increased need to understand the factors driving adult migration mortality and to find reliable information that can both describe and predict migration mortality (Patterson et al., 2017). The management of Fraser River sockeye salmon (*O. nerka*) is one system where there is an acute need to better understand the factors driving en route and pre-spawn mortality (Cohen, 2012; COSEWIC, 2017; Hinch et al., 2012). The existing management structure can readily use this

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information (Patterson et al., 2016) as it is based on an exploitation rate that changes with in-season updates of run size to achieve a target number of spawners. In addition, adjustments to harvest are made to account for the number of fish that are forecasted to be lost due to assessment biases and non-catch mortality between the lower river and their spawning grounds (Macdonald et al., 2010). Causes of mortality include exposure to high temperature, extreme discharge levels, predators, disease, and fishing-related incidental mortality but only some of these are currently modelled (Baker et al., 2014; Gale et al., 2014; Hague and Patterson, 2014; Macdonald et al., 2010; Miller et al., 2014; Patterson et al., 2017). Current post-season descriptive methods to estimate in-river mortality and better understand population status use a combination of environmental-based models (e.g., Martins et al., 2011) as well as direct reports of fish surficial condition from in-river catch monitoring and spawning ground assessment programs (D. Patterson, pers. obs.). For example, if high incidents of injuries are seen during migration, harvest could be adjusted, while a high incident of net wounds or gill necrosis, indicative of high fishing related incidental catch or high temperature impacts respectively, on the catch either in-river or on the spawning ground, could be used to support higher in-river loss estimates for run sizes. For both predictive and descriptive models, there is the potential to also consider the surficial condition of the fish, indicative of pathogens, predators, and fisheries interactions, into estimates of en route mortality (Baker et al., 2011, 2013; Bass et al., 2018a; Macdonald et al., 2000; Patterson et al., 2007).

Endogenous energy reserves accumulated by salmon while feeding in the ocean are used to fuel the maturation of secondary sexual characteristics, osmoregulation, up-river migration, and the production of viable eggs and sperm during the non-feeding in-river migration (Burgner, 1991). Injury can cause physiological stress, reducing the amount of energy available for these other functions (Barton, 2002; Baker et al., 2013; Baker and Schindler, 2009; Bass et al., 2018a; Burgner, 1991; Crossin et al., 2004; Gale et al., 2011). Injury also removes the mucous covering that acts as a protective layer against infections and pathogens (Burgner, 1991; Fast et al., 2002; Svendsen and Bogwald, 1997). Some injuries occur in the ocean or during migration, such as from predators (e.g., seals, sharks; Christensen and Trites, 2011; Forrest et al., 2009), macroparasites (e.g., sea lice, lamprey; Andrew and Geen, 1958; Branson et al., 2018; Johnson et al., 1996; Williams and Gilhousen, 1968;), fishing gear (e.g., gillnets, hooks; Baker and Schindler, 2009; Baker et al., 2011, 2013; Kanigan et al., 2019), and physical structures (e.g., hydraulic challenges in canyons or fishways; Castro-Santos et al., 2009). Other injuries usually occur on the spawning grounds, such as tissue damage from microparasite infection (e.g., fungal, bacterial; Kent, 2011; Neish, 1977; Tierney and Farrell, 2004) and interactions with conspecifics (e.g., spawning behaviour). Known consequences of injuries include reduced spawning success (Bass et al., 2018a; Baker and Schindler, 2009; Baker et al., 2013; Berg et al., 1986) and migration success (Bass et al., 2018a; Hinch et al., 2021). By examining the extent to which we can use pre-spawn migration-related injury scores to predict spawning success or post-spawn injury scores to describe severity of migration conditions, we hope to further refine estimates of in-river mortality (e.g., Baker et al., 2013; Bass et al., 2018a; Bett et al., 2022; Kanigan et al., 2019; Patterson et al., 2017; Raby et al., 2015).

The main objective of this study was to determine how injury assessments of individually tagged sockeye salmon changed during the final stages of migration and during spawning; we are not aware of repeated individual injury assessments being conducted before in semelparous fish. The initial pre-spawn migration-related injury scores of individual fish tagged 45 km from the spawning ground were compared to final scores upon death on the spawning ground (which combines injuries from migration and spawning ground interactions) to determine which types of injuries caused the largest increase in injury scores. Based on previous work, we predicted that gillnet injuries would result in the largest change (Baker and Schindler, 2009; Bass et al., 2018a; Berg et al., **1986**). We also compared migration-related injury scores of individuals tagged on arrival to the spawning ground to those upon their death to better understand how scores change during the spawning period. If injuries inhibit spawning, then females with higher migration-related initial scores should show higher rates of pre-spawn mortality. There is no way to determine whether a male has spawned and so this prediction can only be tested in females. Finally, regardless of where initial pre-spawn migration-related injuries were assessed, if post-spawn injury scores still accurately reflect the severity of migration conditions, then pre-spawn and post-spawn injury scores should be correlated. The findings from this study will elucidate whether qualitative descriptions of fish at or near the spawning grounds can help to further refine modelled estimates of migration severity and pre-spawn mortality.

2. Methods

2.1. Study Location

This study used the Gates Creek population of sockeye salmon and took place in the Seton-Anderson watershed, part of the Fraser River system in British Columbia, Canada (Fig. 1A). The Gates Creek spawning channel is an engineered side-channel of Gates Creek that is approximately one kilometer upstream of Anderson Lake (Fig. 1B). The spawning channel itself is just under two kilometers in length and is a closed system for fish, allowing for near complete recovery of all fish moving into the spawning area (Fig. 1C). Water enters through an inflow at the top of the spawning channel, creating flow conditions similar to those experienced in the adjacent natural environment.

2.2. Data collection

We used two groups of sockeye salmon. The first group (assessed at Seton Dam, hereafter called 'Seton") had an initial injury assessment completed immediately before ascending the Seton Dam ('dam' in Fig. 1B). Fish had to then pass the dam via the fishway where they may have experienced hydraulic-related injuries and migrate through two lakes over a distance of approximately 45 km before either entering the spawning channel or continuing up Gates Creek. Details on physical aspects of the dam and fishway, including photos, can be found in Bett et al. (2022). In this group, only fish that entered the spawning channel were available for final injury assessments. The second group (assessed at Gates Creek, hereafter called 'Gates') was initially assessed when the fish first entered the same spawning channel ('capture' in Fig. 1C), and so were all available for final assessments. In both groups, final assessments were conducted once the fish were found dead or in a moribund state within that same spawning channel. One team performed the initial assessment of Seton fish (pictures taken), while a second team performed the initial assessment of Gates fish (no pictures) and all final assessments (pictures taken; see Results for testing subjectivity in scoring). Initial injury assessments were scored while the fish were being tagged (see below), while final injury assessments were scored later using photographs of both sides of each fish. The entire channel was searched for dead fish one to two times per day and so final injury assessments were conducted within 24 hrs of death.

For the Seton group, initial injury assessments and tagging were conducted August 8–31, 2016. Death and therefore final injury assessment occurred between August 21 and September 22, 2016. Fish were trapped by an in-stream fence and then individually captured using dip nets and brought to a water-filled V-shaped trough at the edge of the river, where initial external injury assessments were performed and sex was determined (see Bass et al., 2018a and Kanigan et al., 2019 for full details, and see Bett et al., 2022 for photos of the fence and sampling trough). Fish were marked with a passive integrated transponder (PIT) tag and an external spaghetti tag inserted through the musculature behind the dorsal fin. The relationship between injury type, survival, and spawning success in the Seton group has previously been published



Fig. 1. A: The province of British Columbia and the main waterway of the Fraser River. B: The Anderson-Seton watershed with the initial assessment points for the two groups, 'dam' for Seton fish and 'channel' for Gates fish. C: Detail of Gates Creek spawning channel and the initial assessment point for Gates group ('capture').

elsewhere (Bass et al., 2018a).

For the Gates group, initial injury assessment occurred between August 24 and September 13, 2016. Final assessments of dead and moribund fish were conducted from August 27 to September 21, 2016. Methods for tagging was similar to the Seton group, except fish were tagged with an external spaghetti tag inserted in the musculature behind the dorsal fin and a Peterson disk tag inserted through the musculature anterior to the dorsal fin. Dead females were checked internally for eggs to assess reproductive success. Individual female spawning success was scored based on estimates of the percentage of eggs retained and a female was considered to be a successful spawner if she released at least 25% of her eggs and an unsuccessful spawner if she retained 75% or more of her eggs.

For all assessment groups, the number of injuries and their overall severity were used to determine an overall injury score (Fig. 2). There were four categories for the overall injury score, indicating increasing severity: no injury (0), minimal injury (1), moderate injury (2), and severe injury (3). No injury was defined as having no external wounds or fungus present on the fish. Minimal injury was defined as having no open wounds, with total injuries covering no more than 5% of the body. Fin damage such as splits, fraying, and small portions missing was included in this category. Moderate injury was defined as damage covering < 20% of the body and included small open wounds, more extensive fin damage, small patches of fungus, and moderate scale loss. One injured eye automatically put the fish in the moderate injury range, as partial loss of eyesight was assumed to have fitness consequences. Severe injury was defined as damage covering > 20% of the body, and included large patches of fungus, extensive open wounds, extensive fin damage, extensive scale loss, and/or skin lesions. Two injured or missing



Fig. 2. Final injury assessments of male sockeye salmon (*Oncorhynchus nerka*). A: injury score of 1 (minimal injury); B: injury score of 2 (moderate injury); C: injury score of 3 (severe injury). Injury score of 0 is not pictured because at final injury assessments, there were no fish in this category.

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eyes automatically put fish in this category. These categories are similar to Baker and Schindler's (2009) categories for gillnet injuries, however, at final assessment (death) scale loss estimates were not included because many fish naturally absorb scales during the last stages of their migration (Burgner, 1991).

We gathered additional information about specific injury type for the Seton group to see if certain injuries were more likely to result in a change in the severity between initial and final injury scores. Initial injury assessments were attributed to damage from gillnets, sea lice, lamprey, hooks, predators, and unknown sources, with injuries on the head classified separately (see Bass et al., 2018a and Kanigan et al., 2019 for similar descriptions). Gillnet injuries were identified by wounds or patterned scale loss along the lateral sides of the fish putatively caused



Fig. 3. Specific injury types observed in migrating sockeye salmon (Oncorhynchus nerka). A: gillnet; B: sea lice; C: lamprey; D: predator.

by the scraping against the net as they swam through the mesh openings, as well as injuries to the dorsal, pelvic, and/or anal fin(s) (Fig. 3A). Sea lice (presumably Lepeophtheirus salmonis) injuries included scars or, if severe enough, open wounds on the caudal peduncle that could extend further up the body to the base of the dorsal fin (Fig. 3B). Injuries from Pacific lamprey (Entosphenus tridentatus) injuries were identified by the characteristic circular epidermal wound left behind after a rasping event (Fig. 3C), though we acknowledge that pathogens may cause similar wounds as well. Hooking injuries from angler events were characterized as a small wound found on the mandible, maxilla, premaxilla, or area around the snout of the fish and often involved a small tear in the tissue. Predator injuries were defined as wounds left from natural predators including brown bears (Ursus arctos), seals, or birds of prey such as bald eagles (Haliaeetus leucocephalus) (Fig. 3D) with mammalian predator wounds consisting of long gashes along the body of the fish and avian-derived wounds consisting of puncture marks. Unknown body injuries were assigned when the origin of the wound was uncertain, or when they had progressed to a state where origin was no longer possible to infer

We classified any injuries to the head in a separate category, due to the more robust nature of the underlying bony skull. Injury types generally varied in their associated degrees of damage. For example, gillnet and sea lice injuries tend to cause more damage and so receive greater scores by being relatively large, and typically consisted of open wounds. These differed greatly in extent from the small punctures on the lips from hook wounds.

Individual injury types were not recorded for the initial assessments for Gates group due to time constraints associated with minimizing handling time and challenges of determining injury types at this late stage of maturation. Injury type was also not recorded in the final assessment of either group as the degradation of tissue and increase in fungal cover rendered most of the initially identified injuries and the origin of new injuries unidentifiable. Thus, only the initial injuries of the Seton group were recorded by type, while their final assessment and both assessments of the Gates group only had the severity of injuries (injury score) recorded.

2.3. Statistical analyses

In all our analyses, to account for the ordinal nature of injury scores, nonparametric tests were used. To test subjectivity between the two teams that performed assessments for the Seton group, the final injury assessor also scored a subsample of pictures taken at initial assessment. A Wilcoxon signed rank test was used to determine whether initial injury scores differed between the two assessment teams. To test repeatability of assessments within a team, final assessments of the pictures were scored two times by the same person with two weeks separating the assessments.

To determine whether fish differed in injury scores between initial assessment locations (Seton vs Gates), we used ordinal regressions with location, sex, and their interaction term as categorical factors and with fish length as a linear covariate. Fish length (fork length for Seton fish, standard length for Gates fish) was included as some injury types may be affected by body size (e.g., gillnets target larger fish: Baker et al., 2011) and sex was included as females are in general more susceptible to fisheries interactions than males (Bass et al., 2018a).

For both groups of fish, we used separate ordinal regression models to test whether sex or body length affected 1) initial injury scores, 2) the differences in injury scores between assessment points, and 3) final injury score, where we also included initial injury score as a categorical predictor. We also tested whether final injury score was related to initial injury score within each assessment location (Seton and Gates) with Spearman's rank correlations. Additionally, for Seton fish, we used ordinal regression to test which types of injury were associated with increases in injury scores between assessment points. Finally, for the Gates group, we used logistic regression to test whether female spawning success was influenced by initial injury score, final injury score, and length.

Analyses were performed using the 'MASS' (Venables and Ripley, 2002) and 'car' (Fox and Weisberg, 2011) packages for R version 4.0.2 (R Core Team, 2021).

3. Results

3.1. Assessment bias

We found no evidence for subjectivity within or between assessors, as there was no statistical difference in the comparison of initial assessment scores for Seton fish from the two teams (Wilcoxon signed ranks test, Z = -1.28, p = 0.20). The repeatability test revealed that there was no significant difference between the injury scores on the same fish assessed by one person two weeks apart (Z = -0.21, p = 0.83).

3.2. Both groups

Initial injury scores did not differ between tagging groups but were higher in females than males with a borderline significant interaction between sex and tagging location (Table 1).

3.3. Seton group

A total of 665 sockeye salmon were initially assessed and tagged at Seton Dam where females had higher initial injury scores than males (Likelihood Ratio $\chi^2 = 14.26$, df = 1661, p = 0.00016; Table 2; median score = 1, range 0–3) (see Bass et al., 2018a for analysis involving the full data set of 665 fish, including spawning success). At death, we recovered 147 salmon from this group in Gates Creek spawning channel, of which 146 had their final injury score recorded, as one carcass had additional post-mortem damage (median score = 2, range 1–3; Fig. 4A). Initial injury score was positively related to final injury score (Spearman's correlation, rho = 0.16, p = 0.050). Three fish (two females and one male) showed a decrease in their injury score from an initial score of 2 to a final score of 1, suggestive of a possible assessment error or recovery/wound healing.

For Seton fish that were found at death in the spawning channel, at initial assessment 12% had no discernible injuries. The most common types of identifiable injuries were gillnets (22%) and sea lice (37%), and 49% had injuries from an unidentifiable source (Fig. 5). Fish with no initial injuries had a greater increase in injury score than fish with gillnet, sea lice, or unidentifiable injuries (LR $\chi^2 = 34.72$, df = 3, p < 0.0001; Tukey contrasts: gillnet vs no injury: z = -4.52, p < 0.001; sea lice vs no injury: z = -3.74, p = 0.001; other injury vs no injury: z = -4.24, p < 0.001; all other contrasts p > 0.23).

Table 1

Ordinal regression model of the variables affecting initial injury scores for sockeye salmon (*Oncorhynchus nerka*) in the Seton and Gates groups (assessment location effect).

Response Variable	Explanatory Variable	df	$LR \ \chi^2$	p- value
Initial injury score (ordinal)	Assessment location Sex	1,726 1, 726	0.12 10.99	0.73 0.0009
	$\begin{array}{l} \text{Length} \\ \text{Assessment location} \\ \times \ \text{Sex} \end{array}$	1,726 1,726	1.25 3.61	0.26 0.057

*Bold font indicates statistical significance (p < 0.05).

*LR = likelihood ratio

Table 2

Three ordinal regression models of the variables predicting injury scores of Seton	
sockeye salmon (Oncorhynchus nerka).	

Response Variable	Explanatory Variable	df	$LR \ \chi^2$	p-value
Initial injury score (ordinal)	Sex	1, 661	14.26	0.00016
	Fork length	1, 661	1.39	0.24
	$Sex \times Length$	1, 661	0.16	0.69
Final injury score (ordinal)	Initial injury score	3, 134	10.54	0.015
	Sex	1, 134	3.70	0.054
	Length	1, 134	0.10	0.76
	Initial score \times Sex	3, 134	0.54	0.90
Injury score difference (ordinal)	Sex	1, 140	0.06	0.44
	Length	1, 140	0.001	0.97

*Bold font indicates statistical significance (p < 0.05).

*LR = likelihood ratio

3.4. Gates group

A total of 66 sockeye were initially tagged at the entrance to Gates spawning channel and all were recovered for final assessment. The median injury score for the initial assessment was 1 (range 0–3) which increased to a median injury score of 3 in the final assessment (range 1–3) (Fig. 4B). Sexes did not differ in initial injury score (Table 3) and initial injury scores were not correlated with final scores (Spearman correlation p = 0.96; Table 3), in contrast with Seton fish. Females that successfully spawned had lower initial (LR $\chi^2 = 7.86$, df = 3,26, p = 0.049) and higher final ($\chi^2 = 13.17$, df = 2,26, p = 0.0014) injury scores than those that experienced pre-spawn mortality (Table 3; Fig. 6). Three fish (two females and one male) had lower final than initial injury scores: two fish had an initial score of 2, which decreased to a final score of 1, and one fish had an initial score of 3, which decreased to a final score of 2.

4. Discussion

The average injury scores for sockeye salmon tagged 45 km from the spawning ground and at arrival to the spawning ground increased between the initial and the final assessment, and was correlated in the Seton group (which had a larger sample size). This suggests that, at an individual scale, injury assessments made on post-spawning fish are likely to reflect conditions prior to their arrival at the spawning grounds. While this suggests that injury assessments on the spawning grounds can be used to describe severity of conditions en route, it is important to remember that while this relationship is true for fish that survive migration, it does not reflect that some fish, especially injured females, die during that time (Bass et al., 2018a). The relationship between final condition and migration experience is also highly dependent on where the initial assessment takes place as there was no correlation in fish initially assessed on arrival to the spawning channel, suggesting that their increase in injury scores was unrelated to migration injuries. Additionally, our study was only conducted in one year, and variation in thermal and flow regimes among years may change these relationships. The 2016 sockeye run in the Fraser River was the lowest in 50 years, and fish experienced below-average discharge and above-average temperature (Pacific Salmon Commission, 2017). Even though low run years may be the most important ones in which to use surficial injury information, harsh migration conditions may have exacerbated injuries, and more highly injured individuals may generate weaker correlations and



Fig. 4. Total number of sockeye salmon (*Oncorhynchus nerka*) that were assigned each injury score in both the initial (black) and final (grey) assessments for fish from (A) Seton Dam (n = 146, initial only includes fish that had final assessment as well), and (B) Gates channel (n = 66). There was a significant increase from the initial to the final injury score in both groups, but no difference between groups.



Fig. 5. Percentage of sockeye salmon (*Oncorhynchus nerka*) from the Seton group with each injury type assigned to each injury category for individuals that were also assessed upon death. Some fish had more than one injury type.

Table 3

Three ordinal regression models and one logistic regression model of the variables predicting injury scores, recapture status, and spawning success of Gates sockeye salmon (*Oncorhynchus nerka*).

Response Variable	Explanatory Variable	df	$LR \ \chi^2$	p- value
Initial injury score (ordinal) Final injury score (ordinal)	Sex Length Initial injury score Sex Length	1, 63 1, 63 3, 56 1, 56 1, 56	0.39 0.003 0.63 0.10 0.38	0.53 0.95 0.89 0.75 0.54
Injury score difference (ordinal) Spawning success (logistic)	Initial score × Sex Sex Length Initial injury score	3, 56 1, 61 1, 61 3, 26	0.042 0.031 0.034 7.86	0.99 0.86 0.85 0.049
	Final injury score	2, 26	13.17	0.0014
	Length Initial x final injury score	1, 26 4,26	1.13 0.27	0.29 0.99

*Bold font indicates statistical significance (p < 0.05).

*LR = likelihood ratio.



Fig. 6. Initial and final injury scores for sockeye salmon (*Oncorhynchus nerka*) from the Gates group that successfully spawned or experienced prespawn mortality.

make assessments less predictive.

When sockeye salmon reach the spawning grounds, their endogenous energy reserves are already heavily depleted by migration (60–86% across Fraser River stocks) and the development of secondary sexual characteristics, eggs, and sperm (Crossin et al., 2004). The remaining energy is used for courting and spawning (Healey et al., 2003), leaving no energy for fighting parasites or infections, as individuals die when they have 3–4 MJ/kg of energy remaining (Bowerman et al., 2017; Crossin et al., 2004; Mesa and Magie, 2006). During senescence, sockeye salmon naturally experience degradation to their overall body condition (Finch, 1990; Hruska et al., 2010; Morbey et al., 2005) and often contract fungal infections (Fagerlund et al., 1995; Neish, 1977). This may exacerbate injuries and wounds that are already present, increasing their severity (Baker and Schindler, 2009). In fact, fungal infections contracted due to injuries before spawning may be a major cause of pre-spawn mortality (Baker and Schindler, 2009), though we cannot separate the effects of other injuries from the effects of subsequent fungal infections in our study. Thus our definition of an injury is general: any damage from predators or parasites (sea lice, lamprey, and fungal species), or from interactions with conspecifics, physical structures, or fishing gear (Baker et al., 2011, 2013; English et al., 2011; Hruska et al., 2010). Sockeye salmon are also highly competitive on their spawning grounds and individuals of both sexes attack intruders (Burgner, 1991; Mathisen, 1962; Quinn and Foote, 1994; Quinn and McPhee, 2005), increasing the number of injuries. However not all individuals experience the same level of competition. For example, some male salmon (usually smaller jacks) exhibit an alternative mating tactic where they sneak fertilizations (Berejikian et al., 2010; Mahranvar, 2002; Young et al., 2013), and male dominance can vary with size within an age class (Fleming and Gross, 1994; Quinn et al., 2001). However, we found no effect of body length on injury scores. Females also experience a variety of interactions that may lead to injury during spawning. Successfully spawning females usually accrue injuries while digging redds and during interactions with other females when defending those redds, while females that fail to spawn do not experience these interactions. In support of this, we found that females that successfully spawned had higher final injury scores than those that did not.

We found that females had higher injury scores than males at the dam (Seton group) but not by the time they reached the spawning channel (Gates group), suggesting that in crossing the dam and lakes, highly injured fish (especially females) died. This is supported by a study showing that sockeye salmon with higher injury scores at Seton Dam were less likely to arrive at Gates Creek (Bass et al., 2018a) and several studies showing in general sockeye salmon with injuries were less likely to survive to spawn (Bass et al., 2018b; Baker and Schindler, 2009; Donaldson et al., 2012; Hinch et al., 2021; Keefer et al., 2008; Nguyen et al., 2014). We also found that initial injury score predicted spawning success in Gates fish, and so our study contributes to the growing evidence that injuries present when entering a spawning area affect reproductive success in females both in this system (Bass et al., 2018a) and elsewhere (Alaskan sockeye salmon: Baker and Schindler, 2009; Atlantic salmon (Salmo salar): Berg et al., 1986). Injured females that spawn could also have lower fitness in other ways. For example, injured Atlantic salmon used different spawning areas than uninjured females (Berg et al., 1986).

We observed 37 fish (17.5%) that did not increase in injury score and six fish (2.8%) that had a lower score at death. For the fish that did not change score, it is possible that their injuries increased in severity or number, but not to an extent where it impacted their overall injury score. This is especially true for fish that were initially scored as 3 (3.8%) since there was no higher score (a ceiling effect). For this type of scoring method to be useful, the injury categories should be expanded to include additional categories for fish with more severe injuries. For the six fish with lower scores that appeared to heal, one hypothesis is that they may have allocated energy towards immune functions and wound repair in order to buy them more time to mature, though the relationship between immunity and maturity is complex (Teffer et al., 2018) and allocating energy towards immunity is usually only present in animals that reproduce more than once (i.e. iteroparous animals: Wingfield et al., 1998). However, limited examples of healing have been observed in recaptured tagged fish (D. Patterson, pers. obs.). Alternatively, lower final scores could be an indication of low levels of incorrect scoring during one of the assessments.

Some types of injuries can have larger effects on reproductive success than others. Gillnet and sea lice were the most common identified injury type and caused minimal to severe damage at initial assessment. Sea lice (primarily *Lepeophtheirus salmonis*) are marine ecto-parasites that attach to the fish and continuously feed on the scales and epithelial mucus cells, inhibiting the production and replenishment of the mucus layer (Costello, 2006; Wagner et al., 2005). Sea lice injuries ranged from mild damage to the top epithelial layer to large, deep open wounds extending into the muscle underneath, and these parasites also depress immune and histological responses (Braden et al., 2015; Øvergård et al., 2022) and can cause mortality (Johnson et al., 1996). Injuries from gillnets were caused by the fish struggling to swim through one of the monofilament mesh opening and scraping off scales, mucus, and sometimes skin (Baker and Schindler, 2009). While we did not identify any specific effects of either type of injury on injury scores, other studies have shown that sockeye salmon with either gillnet marks or sea lice scars were less likely to survive the migration from Seton to spawning grounds (Bass et al., 2018a), females with gillnet marks were less likely to successfully spawn in Gates Creek (Bass et al., 2018a), and fish experimentally subjected to nets at Seton dam took longer to migrate to the creek (Elmer et al., 2022) and experienced greater physiological disturbance (Donaldson et al., 2012). Most research has focused on gill net and sea lice injuries, likely because other types of injuries are found in low numbers or are difficult to identify on fish, and so their effects on survival or spawning are rarely assessed.

Injury assessments on the spawning grounds have been routinely collected by stock assessment crews in the Fraser River for decades (e.g., Schubert, 1998). This information has been used to infer severity of migration conditions and generate support for estimates of en route mortality (Macdonald et al., 2000). Having early injury scores could be useful in helping assess the state of a population and management options, such as fisheries opening/closures (Kanigan et al., 2019). Populations that have a large proportion of injured individuals would be expected to have lower survival and reproductive success (Baker et al., 2014), and closures may be necessary to decrease additional stressors so escapement targets can be met (Gale et al., 2011). The use of early injury scores to decrease the uncertainty in predicting how many fish make it to the spawning grounds was demonstrated by Bass et al. (2018a). However, we would recommend caution against using our definition of maximum injury scores because of the likely ceiling effect which reduced our ability to explore more nuanced aspects of injury. The exact timing of injury assessment would also be crucial, so assessments made from standard mark-recapture studies would likely provide better information on prior migratory severity than carcass surveys given the large deterioration of fish condition in the final days of spawning (Altizer et al., 2013; Crossin et al., 2008; Macdonald et al., 2000; Neish, 1977). Thus the utility of using qualitative assessments of fish surficial condition lies in its ability to use pre-spawn injury scores to predict spawning success, but it is limited in its ability to use post-spawn injury scores to describe severity of migration conditions to inform stock managers in real time.

With the increasing threat of climate change in the Fraser River (Farrell et al., 2008; Martins et al., 2011; Rand et al., 2006) and elsewhere (Beechie et al., 2013; Bowen et al., 2020; Cunningham et al., 2018; McPhee et al., 2009; Schindler et al., 2008; Siegel and Crozier, 2019), additional studies need to assess how this might impact the progression of injuries in individuals, and how the interaction of climate- and injury-related stressors will affect fitness (e.g., Atlas et al., 2021; Bass et al., 2018a; Keefer et al., 2008). There is also a need to better understand injury types and disease dynamics (Baker et al., 2013; Miller et al., 2014) and further refine injury assessments and scoring methods to improve predictive ability when fish are assessed at points that are spatially and temporally separated from their spawning grounds.

CRediT authorship contribution statement

Madison Philipp: Conceptualization, Investigation, Data curation, Writing – original draft. Kathryn Peiman: Conceptualization, Investigation, Data curation, Writing – review & editing, Visualization. Glenn Crossin: Conceptualization, Writing – review & editing, Supervision. Scott Hinch: Conceptualization, Writing – review & editing, Funding acquisition. David Patterson: Conceptualization, Writing – review & editing, Funding acquisition. **Chris Elvidge:** Formal analysis, Data curation, Writing – review & editing, Visualization. **Steven Cooke:** Conceptualization, Writing – review & editing, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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References

- Altizer, S., Ostfeld, R.S., Johnson, P.T.J., Kutz, S., Harvell, C.D., 2013. Climate change and infectious diseases: from evidence to a predictive framework. Science 341 (6145), 514–519.
- Andrew F.J., Geen G.H., 1958. Sockeye and pink salmon investigations at the Seton Creek hydroelectric installation. International Pacific Salmon Fisheries Commission, Progress Report No. 4.
- Atlas, W.I., Seitz, K.M., Jorgenson, J.W., Millard-Martin, B., Housty, W.G., Ramos-Espinoza, D., Burnett, N.J., Reid, M., Moore, J.W., 2021. Thermal sensitivity and flow-mediated migratory delays drive climate risk for coastal sockeye salmon. Facets 6 (1), 71–89.
- Baker, M.R., Schindler, D.E., 2009. Unaccounted mortality in salmon fisheries: nonretention in gillnets and effects on estimates of spawners. J. Appl. Ecol. 46 (4), 752–761.
- Baker, M.R., Kendal, N.W., Branch, T.A., Schindler, D.E., Quinn, T.P., 2011. Selective pressures of non-retention mortality fisheries for salmon. Evol. Appl. 4, 429–443. Baker, M.R., Swanson, P., Young, G., 2013. Injuries from non-retention in gillnet fisheries
- suppress reproductive maturation in escaped fish. PLOS ONE 8 (7), e69615. Baker, M.R., Schindler, D.E., Essington, T.E., Hilborn, R., 2014. Accounting for escape
- mortality in fisheries: implications for stock productivity and optimal management. Ecol. Appl. 24 (1), 55–70. Barton, B.A., 2002. Stress in fishes: a diversity of responses with particular reference to
- changes in circulating corticosteroids. Integ. Comp. Biol. 42, 517–525. Bass, A., Hinch, S.G., Casselman, M.T., Bett, N.N., Burnett, N.J., Middleton, C.T.,
- Patterson, D.A., 2018a. Visible gill-net injuries predict migration and spawning failure in adult sockeye salmon. Trans. Am. Fish. Soc. 147, 1085–1099.
- Bass, A.L., Hinch, S.G., Patterson, D.A., Cooke, S.J., Farrell, A.P., 2018b. Locationspecific consequences of beach seine and gillnet capture on upriver-migrating sockeye salmon migration behavior and fate. Can. J. Fish. Aquat. Sci. 75 (11), 2011–2023.
- Beechie, T., Imaki, H., Greene, J., Wade, A., Wu, H., Pess, G., Roni, P., Kimball, J., Stanford, J., Kiffney, P., Mantua, N., 2013. Restoring salmon habitat for a changing climate. River Res. Appl. 29 (8), 939–960.
- Berejikian, B.A., Van Doornik, D.M., Endicott, R.C., Hoffnagle, T.L., Tezak, E.P., Moore, M.E., Atkins, J., 2010. Mating success of alternative male phenotypes and evidence for frequency-dependent selection in Chinook salmon, *Oncorhynchus tshawytscha*. Can. J. Fish., Aquat. Sci. 67 (12), 1933–1941.
- Berg, M., Abrahamsen, B., Berg, O.K., 1986. Spawning of injured compared to uninjured female Atlantic Salmon. Salmo salar L. Aqua. Res 17 (3), 195–199.
- Bett, N.B., Hinch, S.G., Bass, A.L., Braun, D.C., Burnett, N.J., Casselman, M.T., Cooke, S. J., Drenner, S.M., Gelchu, A., Harrower, W.L., Ledoux, R., Lotto, A.G., Middleton, C. T., Minke-Martin, V., Patterson, D.A., Zhang, W., Zhu, D.Z., 2022. Using an integrative research approach to improve fish migrations in regulated rivers: a case study on Pacific Salmon in the Fraser River, Canada. Hydrobiologia 849, 385–405.

- Bowen, L., von Biela, V.R., McCormick, S.D., Regish, A.M., Waters, S.C., Durbin-Johnson, B., Britton, M., Settles, M.L., Donnelly, D.S., Laske, S.M., Carey, M.P., 2020. Transcriptomic response to elevated water temperatures in adult migrating Yukon River Chinook salmon (*Oncorhynchus tshawytscha*). Cons. Physiol. 8 (1), coaa084.
- Bowerman, T.E., Pinson-Dumm, A., Peery, C.A., Caudill, C.C., 2017. Reproductive energy expenditure and changes in body morphology for a population of Chinook salmon *Oncorhynchus tshawytscha* with a long distance migration. J. Fish. Biol. 90 (5), 1960–1979.
- Braden, L.M., Barker, D.E., Koop, B.F., Jones, S.R., 2015. Differential modulation of resistance biomarkers in skin of juvenile and mature pink salmon, *Oncorhynchus* gorbuscha by the salmon louse, *Lepeophtheirus salmonis*. Fish. Shellfish Immun. 47 (1), 7–14.
- Branson, M.A., Larkin, I., Parkyn, D.C., Francis-Floyd, R., 2018. Disease, injury, and sea louse parasitism rates of Copper River and Prince William Sound Sockeye (Oncorhynchus nerka), Pink (Oncorhynchus gorbuscha), and Chum (Oncorhynchus keta) Salmon. Fla. Sci. 81 (1), 25–32.
- Burgner, R.L., 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). In: Groot, C., Margolis, L. (Eds.), Pacific salmon life histories. UBC Press, Vancouver (British Columbia), pp. 1–118.
- Castro-Santos T., Cotel A., Webb P.W., 2009. Fishway evaluations for better bioengineering: an integrative approach. Challenges for diadromous fishes in a dynamic global environment. Am. Fish. Soc. Symposium 69, 557–575.
- Christensen V., Trites A.W., 2011. Predation on Fraser River sockeye salmon. Cohen Commission Tech. Rep. 8. 129 pages. Vancouver, BC. www.cohensommission.ca.
- Cohen B.I., 2012. The uncertain future of Fraser River sockeye. Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River, Ottawa, ON. 722 pp. http:// publications.gc.ca/collections/collection_2012/bcp- pco/CP32-93-2012-1-eng.pdf.
- COSEWIC., 2017. COSEWIC assessment and status report on the Sockeye Salmon Oncorhynchus nerka, 24 Designatable Units in the Fraser River Drainage Basin, in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xli + 179 pp. (http://www.registrelepsararegistry.gc.ca/default.asp? lang=en&n=24F7211B-1).
- Costello, M.J., 2006. Ecology of sea lice parasitic on farmed and wild fish. Trends Parasit. 22 (10), 475–483.
- Crossin, G.T., Hinch, S.G., Farrell, A.P., Higgs, D.A., Lotto, A.G., Oakes, J.D., Healey, M. C., 2004. Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. J. Fish. Biol. 65 (3), 788–810.
- Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Patterson, D.A., Jones, S.R.M., Lotto, A.G., Leggatt, R.A., Mathes, M.T., Shrimpton, J.M., Van der Kraak, G., Farrell, A.P., 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. Can. J. Zool. 86, 127–140.
- Cunningham, C.J., Westley, P.A., Adkison, M.D., 2018. Signals of large scale climate drivers, hatchery enhancement, and marine factors in Yukon River Chinook salmon survival revealed with a Bayesian life history model. Glob. Change Biol. 24 (9), 4399–4416.
- Donaldson, M.R., Hinch, S.G., Raby, G.D., Patterson, D.A., Farrell, A.P., Cooke, S.J., 2012. Population-specific consequences of fisheries-related stressors on adult sockeye salmon. Physiol. Biochem. Zool. 85 (6), 729–739.
- Elmer, L.K., Moulton, D.L., Reid, A.J., Farrell, A.P., Patterson, D.A., Hendriks, B., Cooke, S.J., Hinch, S.G., 2022. Thermal selection and delayed migration by adult sockeye salmon (*Oncorhynchus nerka*) following escape from simulated in-river fisheries capture. Fish. Res. 251, 106321.
- English K.K., Edgell T.C., Bocking R.C., Link M.R., Raborn S.W., 2011. Fraser River sockeye fisheries and fisheries management and comparison with Bristol Bay sockeye fisheries. LGL LTd. Cohen Commission Tech. Rept. 7: 190p & appendices. Vancouver, B.C. www.cohencommission.ca.
- Fagerlund, U.H.M., McBride, J.R., Williams, I.V., 1995. Stress and tolerance. In: Groot, C., Margolis, L., Clarke, C.W. (Eds.), Physiological ecology of Pacific salmon. The University of British Columbia Press, Vancouver, pp. 459–504.
- Farrell, A.P., Hinch, S.G., Cooke, S.J., Patterson, D.A., Crossin, G.T., Lapointe, M., Mathes, M.T., 2008. Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. Physiol. Biochem. Zool. 81, 697–708.
- Fast, M.D., Sims, D.E., Burka, J.F., Mustafa, A., Ross, N.W., 2002. Skin morphology and humoral non-specific defence parameters of mucus and plasma in rainbow trout, coho, and Atlantic salmon. Comp. BioChem. Phys. Part A 132, 645–657.
- Finch, C.E., 1990. Longevity, Senescence, and the Genome. University of Chicago Press, Chicago, Ill.
- Fleming, I.A., Gross, M.R., 1994. Breeding competition in a Pacific salmon (Coho: Oncorhynchus kisutch): Measures of natural and sexual selection. Evol 48, 637–657.
- Forrest, K.W., Cave, J.D., Michielsens, C.G., Haulena, M., Smith, D.V., 2009. Evaluation of an electric gradient to deter seal predation on salmon caught in gill-net test fisheries. N. Am. J. Fish. Manag. 29 (4), 885–894.
- Fox, J., Weisberg, S., 2011. An R Companion to Applied Regression, 2nd ed. Sage Publications, Thousand Oaks, CA.
- Gale, M.K., Hinch, S.G., Eliason, E.J., Cooke, S.J., Patterson, D.A., 2011. Physiological impairment of adult Sockeye Salmon in fresh water after simulated capture-andrelease across a range of temperatures. Fish. Res. 112, 85–95.
- Gale, M.K., Hinch, S.G., Cooke, S.J., Donaldson, M.R., Eliason, E.J., Jeffries, K.M., Martins, E.G., Patterson, D.A., 2014. Observable impairments predict mortality of captured and released sockeye salmon at various temperatures. Cons. Physiol. 2 (1), cou029.
- Hague, M.J., Patterson, D.A., 2014. Evaluation of statistical river temperature forecast models for fisheries management. N. Am. J. Fish. Manag. 34 (1), 132–146.

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Healey, M.C., Lake, R., Hinch, S.G., 2003. Energy expenditures during reproduction by sockeye salmon (*Oncorhynchus nerka*). Beh 140 (2), 161–182.

- Hinch, S.G., Cooke, S.J., Farrell, A.P., Miller, K.M., Lapointe, M., Patterson, D.A., 2012. Dead fish swimming: a review of research on the early migration and high premature mortality in adult Fraser River sockeye salmon *Oncorhynchus nerka*. J. Fish. Biol. 81 (2), 576–599.
- Hinch, S.G., Bett, N.N., Eliason, E.J., Farrell, A.P., Cooke, S.J., Patterson, D.A., 2021. Exceptionally high mortality of migrating female salmon: a large-scale emerging trend and a conservation concern. Can. J. Fish. Aquat. Sci. 78 (6), 639–654.
- Hruska, K.A., Hinch, S.G., Healey, M.C., Patterson, D.A., Larsson, S., Farrell, A.P., 2010. Influences of sex and activity level on physiological changes in individual adult Sockeye Salmon during rapid senescence. Physiol. Biochem. Zool. 83, 663–676.
- Johnson, S.C., Blaylock, R.B., Elphick, J., Hyatt, K.D., 1996. Disease induced by the sea louse (*Lepeophteirus salmonis*) (Copepoda: Caligidae) in wild sockeye salmon (*Oncorhynchus nerka*) stocks of Alberni Inlet, British Columbia. Can. J. Fish. Aquat. Sci. 53 (12), 2888–2897.
- Kanigan, A.M., Hinch, S.G., Bass, A.L., Harrower, W.L., 2019. Gill-net fishing effort predicts physical injuries on Sockeye salmon captured near spawning grounds. N. Am. J. Fish. Manag, 39 (3), 441–451.

Keefer, M.L., Peery, C.A., Heinrich, M.J., 2008. Temperature-mediated en route migration mortality and travel rates of endangered Snake River sockeye salmon. Ecol. Fresh. Fish. 17 (1), 136–145.

- Kent M., 2011. Infectious diseases and potential impacts on survival of Fraser River sockeye salmon. Cohen Commission Tech. Rept. 1: 58p. Vancouver, B.C. www. cohencommission.ca.
- Macdonald, J.S., Foreman, M.G.G., Farrell, T., Williams, I.V., Grout, J., Cass, A., Woodey, J.C., Enzenhofer, H., Clarke, W.C., Houtman, R., Donaldson, E.M., Barnes D, D., 2000. The influence of extreme water temperatures on migrating Fraser River Sockeye Salmon (*Oncorhynchus nerka*) during the 1998 spawning season. Can. Tech. Rep. Fish. Aquat. Sci. 2326.
- Macdonald, J.S., Patterson, D.A., Hague, M.J., Guthrie, I.C., 2010. Modeling the influence of environmental factors on spawning migration mortality for sockeye salmon fisheries management in the Fraser River, British Columbia. Trans. Am. Fish. Soc. 139 (3), 768–782.
- Mahranvar, L., 2002. A genetic analysis of the mating system of sockeye salmon. Doctoral dissertation. University of British Columbia
- Martins, E.G., Hinch, S.G., Patterson, D.A., Hague, M.J., Cooke, S.J., Miller, K.M., Lapointe, M.F., English, K.K., Farrell, A.P., 2011. Effects of river temperature and climate warming on stock-specific survival of adult migrating Fraser River Sockeye Salmon (*Oncorhynchus nerka*). Glob. Change Biol. 17, 99–114.
- Mathisen, O.A., 1962. The effect of altered sex ratios on the spawning of red salmon. In: Koo, T.S.Y. (Ed.), Studios of Alaska red salmon. Univ. of Washington Press, Seattle, pp. 141–222.
- McPhee, M.V., Zimmerman, M.S., Beacham, T.D., Beckman, B.R., Olsen, J.B., Seeb, L.W., Templin, W.D., 2009. A hierarchical framework to identify influences on Pacific salmon population abundance and structure in the Arctic-Yukon-Kuskokwim region. Am. Fish. Soc. Symp. 70, 1177–1198.
- Mesa, M.G., Magie, C.D., 2006. Evaluation of energy expenditure in adult spring Chinook salmon migrating upstream in the Columbia River Basin: an assessment based on sequential proximate analysis. River Res. Appl. 22 (10), 1085–1095.
- Miller, K.M., Teffer, A., Tucker, S., Li, S., Schulze, A.D., Trudel, M., Juanes, F., Tabata, A., Kaukinen, K.H., Ginther, N.G., Ming, T.J., Cooke, S.J., Hipfner, J.M., Patterson, D.A., Hinch, S.G., 2014. Infectious disease, shifting climates, and opportunistic predators: cumulative factors potentially impacting wild salmon declines. Evol. Appl. 7, 812–855.
- Morbey, Y.E., Brassil, C.E., Hendry, A.P., 2005. Rapid senescence in Pacific salmon. Am. Nat. 166 (5), 556–568.
- Neish, G.A., 1977. Observations on saprolegniasis of adult sockeye salmon, Oncorhynchus nerka (Walbaum). J. Fish. Biol. 10, 513–522.
- Nguyen, V.M., Martins, E.G., Robichaud, D., Raby, G.D., Donaldson, M.R., Lotto, A.G., Willmore, W.G., Patterson, D.A., Farrell, A.P., Hinch, S.G., Cooke, S.J., 2014. Disentangling the roles of air exposure, gill net injury, and facilitated recovery on the postcapture and release mortality and behavior of adult migratory sockeye salmon (*Oncorhynchus nerka*) in freshwater. Physiol. Biochem. Zool. 87 (1), 125–135.
- Øvergård, A.C., Midtbø, H., Hamre, L.A., Dondrup, M., Bjerga, G.E., Larsen, Ø., Chettri, J. K., Buchmann, K., Nilsen, F., Grotmol, S., 2022. Small, charged proteins in salmon louse (*Lepeophtheirus salmonis*) secretions modulate Atlantic salmon (*Salmo salar*) immune responses and coagulation. Sci. Rep. 12 (1), 1–16.
- Pacific Salmon Commission., 2017. Report of the Fraser River Panel to the Pacific Salmon Commission on the 2016 Fraser River sockeye salmon fishing season. Vancouver, BC. 70 pages.

- Patterson, D.A., Macdonald, J.S., Skibo, K.M., Barnes, D.P., Guthrie, I., Hills, J., 2007. Reconstructing the summer thermal history for the lower Fraser River, 1941 to 2006, and implications for adult sockeye salmon (*Oncorhynchus nerka*) spawning migration. Can. Tech. Rep. Fish. Aquat. Sci. 2724, 1–43 (Fisheries and Oceans Canada, Cultus Lake).
- Patterson, D.A., Cooke, S.J., Hinch, S.G., Robinson, K.A., Young, N., Farrell, A.P., Miller, K.M., 2016. A perspective on physiological studies supporting the provision of scientific advice for the management of Fraser River sockeye salmon (*Oncorhynchus nerka*). Cons. Phy. 4 (1), cow026.
- Patterson D.A., Robinson K.A., Lennox R.J., Nettles T.L., Donaldson L.A., Eliason E.J., Raby G.D., Chapman J.M., Cook K.V., Donaldson M.R., Bass A.L., 2017. Review and evaluation of fishing-related incidental mortality for Pacific salmon. DFO Can. Sci. Advis. Sec. Res. Doc. 2017/010. ix + 155 p.
- Quinn, T.P., Foote, C.J., 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon. *Oncorhynchus nerka*. Anim. Beh. 48, 751–761.
- Quinn, T.P., McPhee, M.V., 2005. Effects of senescence and density on the aggression of adult female sockeye salmon. J. Fish. Biol. 52, 1295–1300.
- Quinn, T.P., Hendry, A.P., Buck, G.B., 2001. Balancing natural and sexual selection in sockeye salmon: interactions between body size, reproductive opportunity and vulnerability to predation by bears. Evol. Ecol. Res. 3, 917–937.
- R Core Team., 2021. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-pro ject.org/.
- Raby, G.D., Donaldson, M.R., Hinch, S.G., Clark, T.D., Eliason, E.J., Jeffries, K.M., Cook, K.V., Teffer, A., Bass, Al, Miller, K.M., Patterson, D.A., Farrel, A.P., Cooke, S.J., 2015. Fishing for effective conservation: context and biotic variation are keys to understanding the survival of Pacific salmon after catch-and-release. Integ. Comp. Biol. 55 (4), 554–576.
- Rand, P.S., Hinch, S.G., Morrison, J., Foreman, M.G.G., MacNutt, M.J., Macdonald, J.S., Healey, M.C., Farrell, A.P., Higgs, D.A., 2006. Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. Trans. Am. Fish. Soc. 135 (3), 655–667.
- Schindler, D.E., Augerot, X., Fleishman, E., Mantua, N.J., Riddell, B., Ruckelshaus, M., Seeb, J., Webster, M., 2008. Climate change, ecosystem impacts, and management for Pacific salmon. Fisheries 33 (10), 502–506.
- Schubert N.D., 1998. The 1994 Fraser River Sockeye Salmon, Oncorhynchus Nerka, Escapement. Fisheries & Oceans Canada, Pacific Region, Science Branch.
- Siegel J., Crozier L., 2019. Impacts of climate change on salmon of the Pacific Northwest. National Marine Fisheries Service, NOAA. 73 pages. https://www.webapps.nwfsc.no aa.gov/assets/11/9835_03132020_140127_BIOP-Lit-Rev-2018.pdf.
- Svendsen, Y.S., Bogwald, J., 1997. Influence of artificial wound and non-intact mucus layer on mortality of Atlantic Salmon (*Salmo salar L.*) following a bath challenge with *Vibrio anguillarum* and *Aeromanas salmonicida*. Fish. Shellfish Immunol. 7, 317–325.
- Teffer, A.K., Bass, A.L., Miller, K.M., Patterson, D.A., Juanes, F., Hinch, S.G., 2018. Infections, fisheries capture, temperature, and host responses: multistressor influences on survival and behaviour of adult Chinook salmon. Can. J. Fish. Aquat. Sci. 75 (11), 2069–2083.
- Tierney, K.B., Farrell, A.P., 2004. The relationships between fish health, metabolic rate, swimming performance and recovery in return-run sockeye salmon, *Oncorhynchus nerka* (Walbaum). J. Fish. Dis. 27 (11), 663–671.
- Venables, W.N., Ripley, B.D., 2002. Random and mixed effects. Modern applied statistics with S. Springer, New York, NY, pp. 271–300.
- Wagner, G.N., Hinch, S.G., Kuchel, L.J., Lotto, A., Jones, S.R.M., Patterson, D.A., Macdonald, J.S., Van Der Kraak, G., Shrimpton, M., English, K.K., Larsson, S., 2005. Metabolic rates and swimming performance of adult Fraser River sockeye salmon (*Oncorhynchus nerka*) after a controlled infection with *Parvicapsula minibicornis*. Can. J. Fish. Aquat. Sci. 62, 2124–2133.
- Williams I.V., Gilhousen P., 1968. Lamprey parasitism on Fraser River sockeye and pink salmon during 1967. International Pacific Salmon Fisheries Commission, Progress Report No. 18.
- Wingfield, J.C., Maney, D.L., Breuner, C.W., Jacobs, J.D., Lynn, S., Ramenofsky, M., Richardson, R.D., 1998. Ecological bases of hormone-behavior interactions: the "emergency life history stage.". Am. Zool. 28, 191–206.
- Young, B., Conti, D.V., Dean, M.D., 2013. Sneaker "jack" males outcompete dominant "hooknose" males under sperm competition in Chinook salmon (*Oncorhynchus tshawytscha*). Ecol. Evol. 3 (15), 4987–4997.