

# Exceptionally high mortality of adult female salmon: a large-scale pattern and a conservation concern

Scott G. Hinch, Nolan N. Bett, Erika J. Eliason, Anthony P. Farrell, Steven J. Cooke, and David A. Patterson

**Abstract:** In recent decades, the relative proportion of female sockeye salmon (*Oncorhynchus nerka*) on spawning grounds of several British Columbia populations has declined. Coincident with the decline has been large changes to oceanic, estuarine, and river migration environments. Over the past 30 years, numerous telemetry tracking and laboratory studies have examined mortality of adult Fraser River sockeye salmon during ocean and freshwater migrations. We reviewed 19 studies that provided 40 situations where male and female mortality could be directly compared. Female mortality averaged 2.1 times greater than that of males and up to eightfold higher. High female mortality was also evident in migrating coho salmon (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) and for sockeye salmon in other systems. Female mortality was highest when migration conditions were challenging (e.g., high or turbulent flows, high temperatures, confinement, or handling) and towards end of river migration. We review mechanisms for differential mortality, including energy exhaustion, cardiac performance, physiological stress, and immune factors. Female-specific mortality will become even more pronounced in coming years as ocean and riverine conditions continue to change.

**Résumé :** Au cours des dernières décennies, la proportion relative de saumons sockeyes (*Oncorhynchus nerka*) femelles dans les frayères de plusieurs populations britanno-colombiennes a diminué. D'importantes modifications des milieux de migration océaniques, estuariens et fluviaux ont coïncidé avec cette baisse. Au cours des 30 dernières années, de nombreuses études de suivi télémétrique et de laboratoire ont examiné la mortalité des saumons sockeyes adultes du fleuve Fraser durant les migrations océaniques et en eau douce. Nous avons passé en revue 19 études qui font état de 40 situations pour lesquelles une comparaison directe de la mortalité des mâles et des femelles est possible. La mortalité des femelles est en moyenne 2,1 fois, et jusqu'à 8 fois, plus grande que celle des mâles. Une forte mortalité des femelles est également évidente chez les saumons cohos (*Oncorhynchus kisutch*) et chinooks (*Oncorhynchus tshawytscha*) en migration et chez les saumons sockeyes dans d'autres réseaux. La mortalité des femelles est au plus fort quand les conditions de migration sont difficiles (p. ex. écoulement fort ou turbulent, températures élevées, confinement ou manipulation) et vers la fin de la migration en rivière. Nous passons en revue les mécanismes expliquant cette mortalité différentielle, dont l'épuisement de l'énergie, la performance cardiaque, le stress physiologique et des facteurs immunitaires. La mortalité des femelles deviendra encore plus prononcée dans les années alors que la modification des conditions océaniques et fluviales se poursuivra. [Traduit par la Rédaction]

## Introduction

Sex ratios are fundamental to the demographics and characteristics of populations (Hardy 2002). The number of females relative to males can influence population growth, sexual selection, mating systems, behaviour, migration strategy, and lifetime productivity (Donald 2007). Among adults, sex ratio can affect reproductive behaviours, such as polygyny, extra-pair copulations, mate-guarding, and cooperative breeding (Donald 2007), as well as ecology and life history (Székely et al. 2014). Skewed adult sex ratios are common in nature and occur across many taxa (Clutton-Brock and Iason 1986; Stoks 2001; Aresco 2005; Christie et al. 2006). In many instances, skewed adult sex ratios result from the persistence of

differences in sex ratios that originate in offspring (Wilson 1975), or they reflect differences in age at maturity (Lovich and Gibbons 1990), with adult sex ratios skewed toward the earlier-maturing sex. There is also evidence, however, that skewed adult sex ratio can be caused by differential mortality between sexes (Rodd and Reznick 1997; Donald 2007; Arendt et al. 2014; Székely et al. 2014).

In fish, sex-specific differences in mortality may be due to differences in predation rates (Britton and Moser 1982; McKellar et al. 2009; Reichard et al. 2014), responses to environmental change (Pettersson et al. 2004), susceptibility to parasitism (Arnold et al. 2003), or one sex having a naturally longer lifespan than the other (Arendt et al. 2014). Differential mortality could have a particularly strong effect on migratory fish with a semelparous

Received 5 October 2020. Accepted 2 January 2021.

**S.G. Hinch and N.N. Bett.** Pacific Salmon Ecology and Conservation Laboratory, Department of Forest and Conservation Sciences, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

**E.J. Eliason.\*** Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93106-9620, USA.

**A.P. Farrell.** Faculty of Land and Food Systems, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

**S.J. Cooke.** Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, ON K1S 5B6, Canada.

**D.A. Patterson.** Fisheries and Oceans Canada, Science Branch, Cooperative Resource Management Institute, School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada.

**Corresponding author:** Scott Hinch (email [scott.hinch@ubc.ca](mailto:scott.hinch@ubc.ca)).

\*Erika Eliason served as an Associate Editor at the time of manuscript review and acceptance; peer review and editorial decisions regarding this manuscript were handled by Keith Tierney.

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from [copyright.com](http://copyright.com).

life history (i.e., die after spawning) because mortality during migration results in zero lifetime fitness. Semelparous Pacific salmon (*Oncorhynchus* spp.) are an especially useful case study because adults do not feed (relying on stored energy) during the river migration and are approaching senescence, and their spawning runs are varied in terms of hydraulic and energetic challenges (e.g., as short as a few kilometres from the ocean and as long as 1150 km (Amur River, northeast Asia — chum salmon, *Oncorhynchus keta*) and 3200 km (Yukon River, northwest North America — Chinook salmon); Brett 1995; Eiler et al. 2015). Indeed, differential sex ratios have been observed in migrating adults in several species, including coho salmon (*Oncorhynchus kisutch*; Holtby and Healey 1990; Spidle et al. 1998), Chinook salmon (*Oncorhynchus tshawytscha*; Olsen et al. 2006), sockeye salmon (*Oncorhynchus nerka*; Barnaby 1944; Foerster 1954; Kendall and Quinn 2013), and masu salmon (*Oncorhynchus masou*; Tamate and Maekawa 2004). Differential sex ratios in spawning Pacific salmon has been hypothesized to originate during or after their ocean life because despite an equal sex ratio for out-migrating smolts (when juvenile salmon leave fresh water for the ocean), several studies note skewed sex ratios of adults on spawning grounds (Barnaby 1944; Foerster 1954; Spidle et al. 1998; Olsen et al. 2006). It is possible that differences in sex ratios may be attributed in part to differences in age at maturity (i.e., if one sex matures later, then relatively fewer individuals will survive to the stage of return migration; Barnaby 1944; Olsen et al. 2006), but the rate of mortality can also differ between sexes (Foerster 1954; Spidle et al. 1998; Tamate and Maekawa 2004). Holtby and Healey (1990) theorized that sex-specific differences in foraging strategies could cause differential mortality rates in the ocean and contribute to skewed adult sex ratios. However, the extent and location of this sex-specific mortality remains largely unexplored for most species of Pacific salmon and in fact most species of anadromous fish. Moreover, few studies have examined whether sex ratios of mature fish have been shifting over the long term, an issue that is particularly important given global environmental change.

### Fraser river sockeye salmon: a case study

We use British Columbia's Fraser River sockeye salmon (*O. nerka*) as a case study to explore the issue of sex-specific mortality in adult Pacific salmon. The Fraser River is Canada's largest producer of salmon. It flows 1375 km and is relatively "wild" having no dams along its main stem and only a couple on its tributaries. Of the five semelparous species of Pacific salmon native to this area, sockeye salmon is the second most abundant and most economically valuable (BCMOA 2017); nearly all sockeye are naturally produced (do not come from hatcheries). There are ~90 geographically isolated spawning populations of Fraser sockeye salmon, with most of the production coming from 10–20 large populations (Beacham et al. 2004).

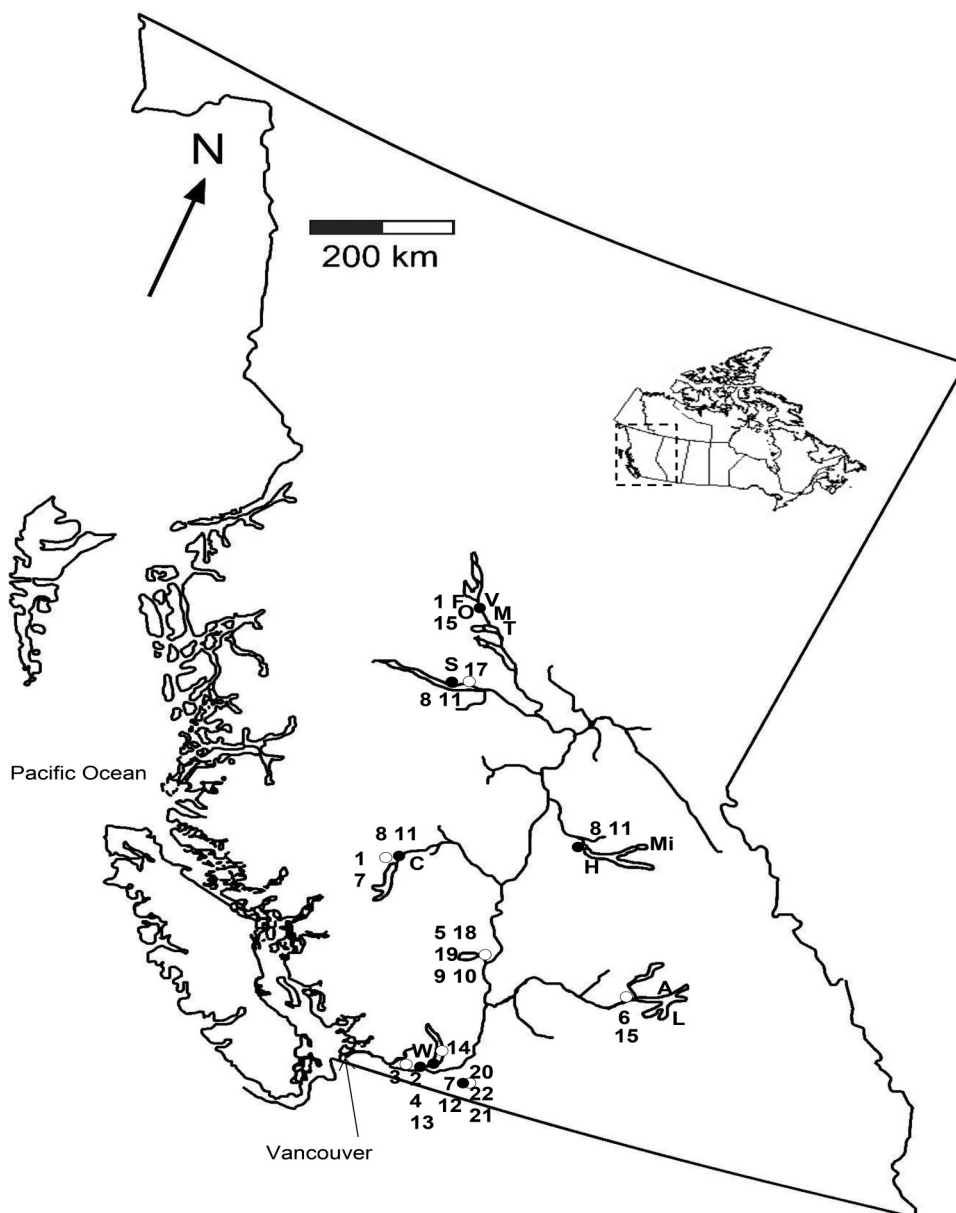
Early research (1929–1937) conducted on sex ratios for the Cultus Lake population of sockeye salmon in the Fraser River (Fig. 1) revealed an even sex ratio for outmigrating smolts (Foerster 1954) but provided strong evidence of a skew towards adult male mortality based on returns to spawning grounds (Foerster 1954). This adult male mortality skew was found in other river systems with sockeye salmon (e.g., Karluk River, Alaska— Barnaby 1944; Babine Lake, British Columbia— Ano 1952; Bristol Bay populations, Alaska— Kendall and Quinn 2013). Indeed, records from the late 1930s to the early 1990s of adult Fraser River sockeye salmon returns across numerous populations generally indicate strong mortality selection against adult males (only 2%–10% of the years have relatively higher male abundance; Fig. 2). Causes for this historical phenomenon are unclear, but the available evidence suggests that differential mortality between sexes is occurring after juveniles leave fresh water. Foerster (1954) examined the possibility that the extensive gillnet fishery in the Fraser River could be a factor by marking outmigrating sockeye smolts and assessing returning adults captured in the

gillnet fishery. He concluded that differential capture of males in the fishery did not occur at a scale that could explain the high number of adult females found in spawning areas. Similarly, Kendall and Quinn (2013) found female-dominated sex ratios on the spawning grounds of several Bristol Bay sockeye salmon populations, which were not fully explained by increased fisheries capture of males. Although the skewed sex ratio was exacerbated by differential fisheries captures, there was already a small but substantial female skew in fish arriving at the location of the fisheries. Experimental evidence in other salmonids suggests that males exhibit higher aggression and bolder behaviours (Jonsson et al. 1991), which may be linked to higher predation risk and mortality (Biro et al. 2003). Furthermore, male sockeye salmon are larger-bodied (Fig. 3; Burgner 1991) and tend to be more erratic swimmers (Hinch and Rand 1998), potentially increasing their visibility to predators and rate of depletion of finite energy reserves.

While historical evidence from the Fraser River and other systems suggests a consistent pattern of a skew towards adult male mortality, it is not a new observation that migratory stressors may have a disproportionate effect on female salmon. In 1913, a major rock slide at Hells Gate in the Fraser River Canyon ~250 km from the ocean blocked the upriver migration of most adult sockeye salmon by creating velocity barriers. Eye witness accounts as detailed by Ricker (1987) reported that downstream of the slide female sockeye salmon appeared lethargic and could be easily captured from the riverside by "gloved hand", whereas males could not be easily seen and could only be captured by gaffing. Males dominated spawning streams and the few females that arrived died without spawning. The removal of some slide material the following year allowed passage to resume although passage issues persisted depending on water discharge. Fishways were constructed at this site 30 years later, which helped in the rebuilding of the upper Fraser sockeye stocks.

In recent decades, there has been a decline in the relative proportion of female sockeye salmon on spawning grounds of several Fraser River populations (Fig. 2). In some species and regions, the average size of adults has been declining over the past several decades, which has also led to a shift towards a younger age of maturity (e.g., Pacific salmon in Alaska; Lewis et al. 2015; Oke et al. 2020), and this could affect sex-specific mortality rates. Yet with Fraser River sockeye, there is no evidence that there has been a consistent trend over time in changes in age of maturation, and in most populations >98% of spawning adults are 4-year-olds, with only a small proportion of 3- or 5-year-olds. The decline in proportion of female sockeye salmon on spawning grounds has, however, coincided with large changes to oceanic, estuarine, and river migration environments related to various aspects of climate change. Since the early 1980s, summer sea surface temperatures in coastal British Columbia and adjacent open ocean rearing areas have warmed by 1.5 °C, reaching summertime highs of 16 and 14 °C, respectively (Metabase Explorer 2019). Although these temperatures are not "lethally high" and in fact are in a range of metabolic thermal optima for many Fraser River sockeye salmon populations (Eliason et al. 2011), this type of thermal change can have considerable sublethal negative effects on growth (which ultimately affects the starting energy stores of migrating salmon) through broader ecosystem changes such as lower prey availability, higher competition (Connors et al. 2020), and potentially higher predation rates (Martins et al. 2012a). One of the largest environmental changes now experienced by Fraser River sockeye salmon concerns their estuarine and upriver migration environment. Peak summer temperatures in the Fraser River, when most populations of adult sockeye are migrating, have warmed by >2 °C over the past 70 years (maximum mean daily temperature in 1950 was 18 °C, and in 2015 it was 20 °C; DFO 2019). Summer temperatures now routinely exceed lethal levels (e.g., >19 °C) during the migration of several populations (Eliason et al. 2011). Indeed, telemetry tracking programs for the Fraser and Columbia rivers

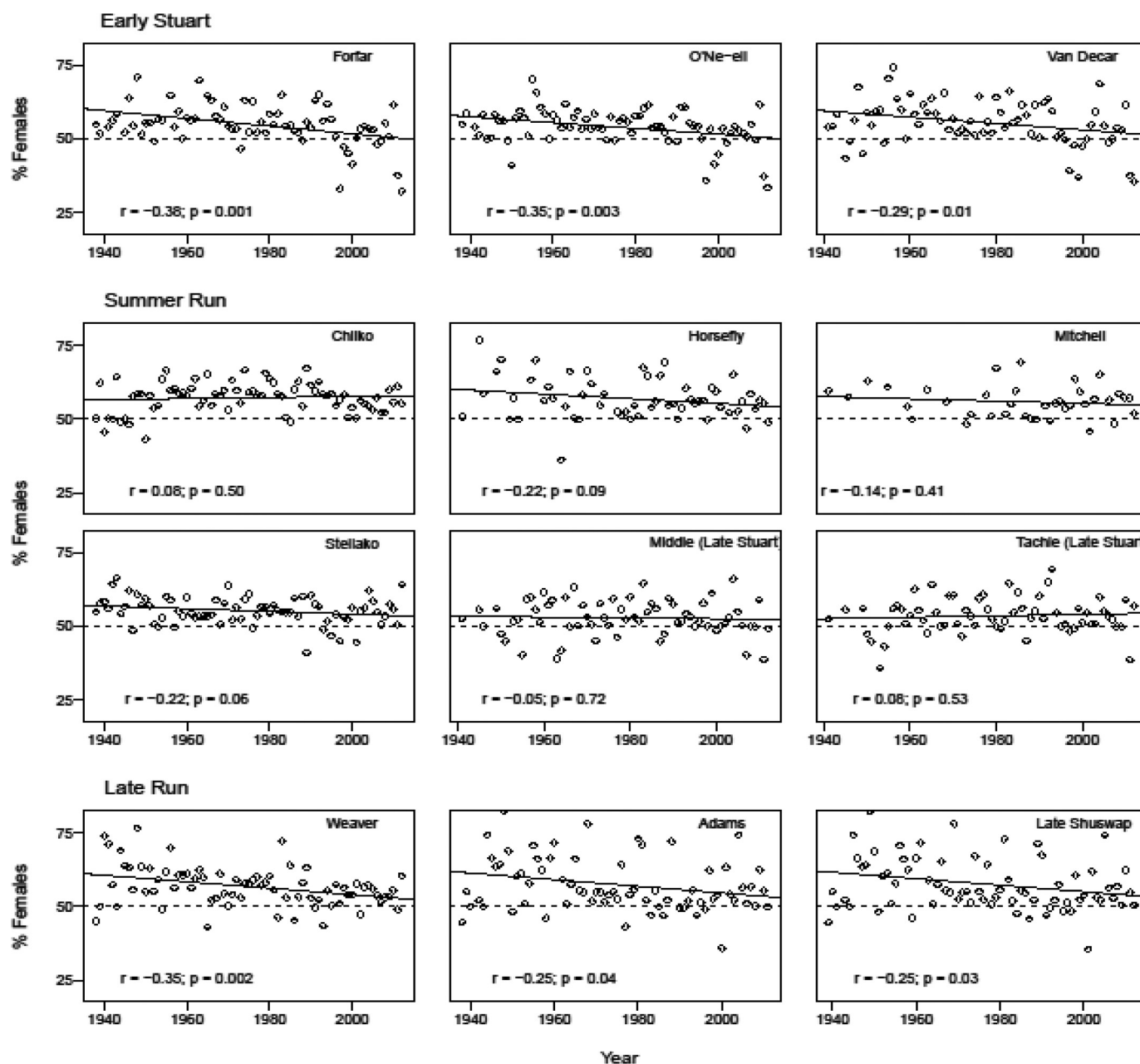
**Fig. 1.** Map of British Columbia, with inset map of Canada, showing the Fraser River main stem, major tributaries, and lake systems. Letters indicate the location of a particular population's spawning stream whose percent female spawner data are presented in Fig. 2: W = Weaver, A = Adams, L = Late Shuswap, C = Chilko, H = Horsefly, Mi = Mitchell, S = Stellako, M = Middle, T = Tachie, V = Vandecar, O = Oneil, F = Forfar. Circles indicate a spawning area for populations of migrating sockeye salmon that were examined in studies which we reviewed (Table A1) — black circles indicate a laboratory study, and white circles indicate a field telemetry study. Numbers correspond to the studies listed in Table A2. Map was modified from Whitney et al. (2014) and Martins et al. (2012b).



consistently show that high temperatures in recent decades have caused high levels of migration mortality in adult Pacific salmon (Keefer et al. 2018; Martins et al. 2011). Migration mortality estimates of 18 million adult sockeye salmon from 1996 to 2015 in the Fraser River have been associated with adverse migration conditions, primarily driven by high water temperature (Patterson et al. 2016). River flow patterns have also changed in the Fraser River. Discharge encountered by upriver migrating sockeye is far more variable than it once was (DFO 2019), and extreme high discharge-related flows have contributed directly to migration mortality in some Fraser sockeye populations (Rand et al. 2006). Also, novel pathogens that may be more virulent at higher temperatures have been associated with altered migration timing and

survival of some sockeye salmon populations (Miller et al. 2011; Hinch et al. 2012). Lastly, although fish harvesting in recent decades has been substantially reduced, locations of some of this harvest have shifted from relatively cool coastal areas to warmer estuarine and riverine areas to address issues associated with Indigenous fisheries (DFO 2001). The unintended consequence of this shift is that mortality associated with fish handling can be much higher in warm estuarine or riverine water (Martins et al. 2011). Thus, fish intentionally released or escapees from fishing gear, which can represent a large number of fish in some years (Bass et al. 2018b), must now cope with warmer temperatures, altered river flows, and more pathogen-laden environments (Teffer et al. 2017).

**Fig. 2.** Percentage of sockeye salmon females observed on the spawning grounds of 12 Fraser River populations. The locations of the spawning grounds are provided in Fig. 1. Populations are categorized by Fraser River run-timing groups. In general, upriver migration occurs during July and early August for the Early Stuart runs, during August for the summer runs, and during September and early October for the late runs. A linear regression line of best fit, correlation coefficient ( $r$ ), and  $p$  value are provided for each population to demonstrate long-term trends. The Early Stuart runs and late runs all show declining percentages of females (1938–2012; all  $p \leq 0.04$ ). The summer runs do not show this same consistent temporal pattern, though declines are suggested for some populations. In all populations, >98% of spawning adults are 4-year-olds, with a small proportion of 3- or 5-year-olds. These particular 12 populations are presented because they are some of the largest Fraser sockeye populations and had the most consistent and longest temporal data.



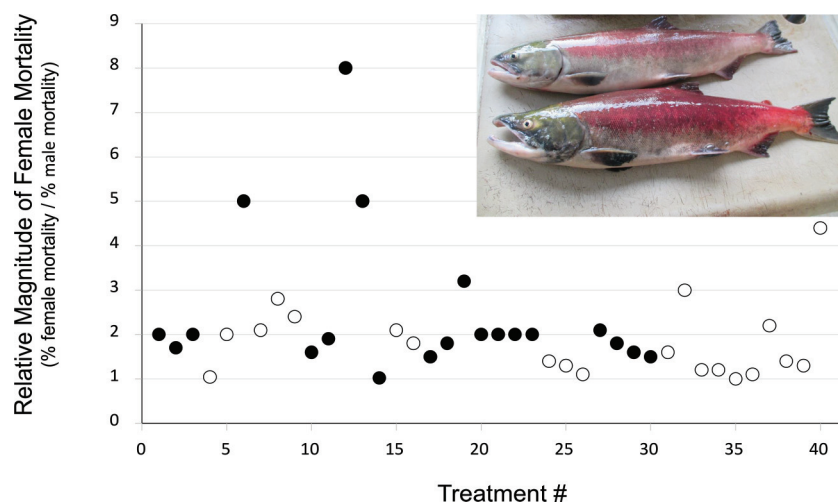
The fact that females historically have outnumbered males on spawning grounds does not mean there has been lost reproductive potential in those situations. On the contrary, microsatellite analyses of genetic reproductive success in Fraser River sockeye salmon have found that individual males will mate successfully (i.e., sire offspring) with on average two, but often up to four, females during their brief breeding period (Mehranvar et al. 2004). The consequences on reproductive behaviour, competition among males for mates, and success of breeding is unclear when males begin to dominate spawning grounds. However, it is

believed that the abundance of spawning female sockeye salmon is an important contributor to population trends (Gilhousen 1990).

In view of the recent shift towards relatively fewer females arriving at several major spawning areas for Fraser River sockeye salmon (Fig. 2) alongside the new and more extreme environmental stressors faced by migrating Pacific salmon both in the ocean and in fresh water, the main focus of our review is to examine how environmental stressors can have a higher impact on the survival of adult female Pacific salmon compared with males. The authors of this paper have been running a large integrated



**Fig. 3.** The relative magnitude of female adult sockeye salmon mortality (% female mortality/% male mortality) across 40 situations (Treatment # — see Table A2) where male and female mortality could be directly compared based on a specific treatment. These results were extracted from 19 published studies. The absolute male and female mortality levels, the experimental “stressors” that were involved in each study, the study’s general design, the identification of the population or run timing group, the population’s natal areas, and brief citation of each study are presented in Table A2. Inset photo is a maturing Summer-run Fraser River sockeye salmon female (top) and male (bottom). Photo taken in 2017 on fish that were captured in the lower Fraser River during the start of the freshwater migration phase, 1–2 weeks prior to arrival on spawning grounds and taken to the Cultus Lake Laboratory for experiments. Mean fork length and mass in that study was, respectively, 56.2 cm and 1.9 kg for females ( $n = 137$ ) and 57.1 cm and 2.1 kg for males ( $n = 111$ ). The photo shows the typical relative differences between sexes in size and morphology with male secondary sexual characteristics becoming evident (e.g., kype at rostrum and dorsal hump). Photo courtesy of David Moulton. [Colour online.]



research program over the past 30 years that has examined mortality patterns of maturing and spawning adult salmon. We reviewed 19 studies from our program on migrating adult Fraser River sockeye salmon that have examined sex as a factor of mortality during their maturing migratory life phase (nearly all are in peer-reviewed outlets; Table A1). We also reviewed two Fraser River studies that involved other salmonid species. Studies varied in their scope (Table A2), approaches, locations (Fig. 1), populations, and techniques, but share in common the fact that sex was assessed as part of the study’s design. Sex is easy to visually distinguish on salmon as they approach or are on spawning grounds (Fig. 3), but much harder during most of the ocean and freshwater upriver migration, something that has limited the study of sex-specific mortality in anadromous fish. However, all of the field tracking studies we reviewed used blood samples taken at the time of fish tagging as a means to identify sex from reproductive hormone titres, thereby overcoming this issue. This radioimmunoassay approach measures plasma testosterone, 17 $\beta$ -estradiol, and 11-keto testosterone levels and is extremely accurate in terms of sex assignment. It has been used since the 1980s and is sensitive to picogram hormone levels (McMaster et al. 1992).

In the laboratory studies we reviewed, fish were dissected at the conclusion of the study to identify sex if it could not be identified visually. Our goals of this review are to help elucidate the common trends of high female mortality, identify the potential mechanistic explanations for the phenomenon, examine how some populations may be more resilient to factors leading to high female mortality, and discuss the potential management and conservation implications of this phenomenon.

## Evidence of high female mortality during sockeye salmon migrations

### Lab-based studies

Laboratory holding experiments have provided considerable and consistent evidence for a differential female mortality phenomenon. In these studies, wild salmon were captured in the

estuary or the Fraser River during their return migration, then transported to nearby research facilities, where they were individually tagged and held in flow-through tanks or raceways. Results and details of these experiments are provided in Table A2. Patterson et al. (2004) captured adult Early Stuart sockeye salmon in the lower Fraser River and held them in cool water tanks for 25 days with and without active flows to examine maturation rates. These fish were bound for spawning areas > 1000 km further upriver (Fig. 1). At the end of the experiment, irrespective of treatment, female mortality was twice that of males. Adult Weaver Creek sockeye (Fig. 1), held for 24 days at either 10 or 18 °C, again resulted in female mortality roughly twice that of male mortality at both holding temperatures (10 °C: 24% of females compared with 14% of males; 18 °C: 44% of females compared with 22% of males; Crossin et al. 2008). The Weaver Creek sockeye salmon were bound for a spawning area just 5 km upriver of the capture site. Similarly, adult sockeye salmon from the nearby Harrison River population (Jeffries et al. 2012a) were held for 10 days at 13 and 19 °C, with females exhibiting almost twice (92%) the mortality of males at 13 °C and a 62% higher mortality than males at 19 °C. Nadeau et al. (2010) conducted a holding experiment with adult Weaver Creek sockeye salmon that were exposed for 18 days at a cool temperature (12 °C) to either slow- or fast-flowing water flows in raceways. In both years this study was performed, females had higher mortality in both flow treatments, although the water speed treatment did not affect survival. In total, female mortality ranged from 37% to 55% across years and treatments, whereas male mortality ranged from 6% to 20% (Nadeau 2007), which suggests that some types of handling of migrating females may have large effects on their survival.

The effects of exhaustive exercise, air exposure, and injury on sockeye survival were examined in several laboratory studies that simulated various aspects of exhaustive exercise, catch-and-release angling, or net fisheries encountered during their upriver migration. Gale et al. (2014) subjected Weaver Creek sockeye to exhaustive exercise and 1 min of air exposure (manually chasing

fish in a circular tank and exposing them to air for 1 min) and then held fish at different temperatures for 2 days. Again, female mortality was approximately twice that of males at all holding temperatures (19 °C: 40% female, 20% male; 16 °C: 20% female, 10% male; 13 °C: 12% female, 6% male). A similar experiment using a mix of summer-run sockeye (Chilko, Stellako, and Late Stuart populations; Fig. 1) attempted to revive fish with “assisted ventilation” as a treatment (holding the fish into the current for 1 min to encourage ventilation) following the exhaustive exercise and air exposure event (Robinson et al. 2013). After being held for 15 days at 16 °C, mortality in females that experienced the simulated capture with or without assisted ventilation was 75% and 100%, respectively. Mortality in males, on the other hand, ranged from only 10% to 30% across all treatment groups.

Recent laboratory studies have introduced actual encounters with fishing gear. Teffer et al. (2017) subjected Early Stuart sockeye salmon to mild (20 s) or severe (20 min) gillnet entanglement, followed by a 1 min air exposure. Fish were held in temperatures that reflected the actual temperature they would have encountered, day to day, had they been left in the river to migrate their 3-week 1100 km upriver journey to spawning grounds (temperature ranged from 12 to 19 °C, though was mostly ~16 °C). At the completion of the 3-week study, mortality among females was ~1.5–1.6 times higher than that for males for each entanglement treatment (70% female mortality and 44% male mortality following mild entanglement and 90% female mortality and 62% male mortality following severe entanglement). Female mortality was over twice as high as males in both control groups: biopsied but not gillnetted (60% females, 33% males) and nonbiopsied controls (7% in females, 15% in males), again, revealing that females do not cope well even with only modest stressors — in this case mild levels of handling.

### Field-based results

Field studies, including those involving minimal handling and no captivity but using a variety of tracking techniques to follow fish migration success, confirm the skew towards female mortality seen in laboratory-based studies. These studies generally have intercepted returning adults in coastal or freshwater environments, fitted them with electronic transmitters (e.g., acoustic, radio-, or passive integrated transponder (PIT) tags), and tracked them as they migrate in ocean and river locales en route to spawning areas. These field study details and results are overviewed in Table A2.

Two studies demonstrated that high temperatures produce differential mortality between sexes. Crossin et al. (2008) implanted sockeye salmon with acoustic transmitters following the laboratory holding treatment described above wherein fish were held for 24 days at either 10 or 18 °C and then released into the river to track survival to the spawning areas. There was no sex-specific difference in migration mortality to spawning grounds among those held in 10 °C water prior to release, but in the 18 °C treatment group, migration mortality was about twice as high in females (87% mortality in females, 44% in males). Most of this migration mortality occurred during the final 10 km of the 70 km migration. Similarly, temperature was a strong contributing factor to higher mortality for females in a study by Martins et al. (2012b), who used capture–mark–recapture modelling approaches to investigate migration mortality rates. Over 400 Fraser River sockeye salmon were radio-tagged and tracked along their 413 km migration. When the river was warm (19 °C), overall freshwater migration mortality was 1.6 times higher in females than in males. As with the findings of Crossin et al. (2008), this sex-specific difference in mortality occurred towards the end of the migration — in this case the final 186 km. Migrants travelling in cooler waters, however, did not exhibit differential mortality rates between sexes.

Disproportionate female mortality after release from exhaustive exercise in fishing gear occurred in field studies as it did in lab studies. Robinson et al. (2015) intercepted adult Weaver Creek and Harrison Rapids sockeye salmon and simulated a capture

event similar to Robinson et al. (2013), using assisted ventilation for 1 min prior to release and tracking with radio-tags. No females subjected to the capture event, with or without assisted ventilation, survived to spawning grounds, and mortality rates in males were also high (with or without assisted ventilation; 92% and 81%, respectively). For control fish that were tagged and released immediately, 74% of females died compared with 47% of males, confirming differential female mortality even for a modest stressor of immediate capture and release. Bass et al. (2018b) used radio-telemetry to examine the effects to several different populations of Fraser sockeye of release from drift gillnet and beach seine fisheries in the lower Fraser on their survival to spawning grounds ~450 km from ocean and a 2- to 3-week migration. For populations that migrate in fall when river temperatures were cooler and approached population thermal optima (Eliaison et al. 2011), overall mortality following release was higher for females than for males independent of fishing gear (gillnet mortality: females 81%, males 50%; beach seine mortality: females 30%, males 10%; Table A2; Bass et al. 2018b). However, for populations migrating upriver in the summer when river temperatures were approaching lethally high levels (Eliaison et al. 2011), all released fish from gill nets of both sexes perished before reaching spawning grounds, as did nearly all fish released from beach seines (80%–85%), with no evidence of sex differential mortality.

Hydropower systems and associated dams are another challenge for migrating Pacific salmon. Although fishways and fish ladders are often in place to facilitate passage of adults over dams, high discharge and turbulent flows near the dam can create velocity barriers that limit the effectiveness of these passage structures (Roscoe and Hinch 2010; Cooke and Hinch 2013). Roscoe et al. (2011) captured returning adult sockeye salmon at the top of a fishway at the Seton River Dam, a tributary of the Fraser River located ~300 river km from the ocean (Fig. 1). Captured fish were tagged with acoustic transmitters, released downstream of the dam, and tracked for ~50 km to spawning areas. Female migration mortality to spawning grounds was twice that of males (61% versus 29%). At the same site but in a different year, Burnett et al. (2014a) used acoustic accelerometer transmitters to track individuals to spawning grounds and also to estimate anaerobic swimming activity during fishway passage. Female migration mortality to spawning grounds was 1.5 times that of males (56% in females and 31% in males). Interestingly, females swam with more anaerobic effort in the high flows of the dam tailrace, and this was attributed as a major factor in their elevated postpassage mortality. Higher anaerobic effort in females relative to males was found in another study using acoustic accelerometer transmitters in the same system (Burnett et al. 2014b).

Hydropower systems can alter water characteristics that are important for homing, and these could have sex-specific effects on Pacific salmon migrations. Salmon rely on unique chemical signatures of their natal sites as directional cues during the upriver spawning migration (Hasler and Scholz 1983), and sockeye exhibit a high level of natal site fidelity (Keefer and Caudill 2014). In some regulated systems, like the Seton River discussed above, altered water flow release patterns can lead to the dilution of natal water, affecting the attraction of salmon. Drenner et al. (2018) conducted a large whole-river experiment in the Seton River, diluting the concentration of natal water through the diversion of a non-natal river. Sockeye were captured at the Seton River Dam, transported 6 km downstream to the Fraser River main stem, radio-tagged, and tracked back into the Seton River under diluted or nondiluted natal river conditions. For nondiluted conditions, nearly all of the fish (96%–97%) re-entered the Seton River. Yet, under diluted conditions, only 69% of females re-entered, whereas 93% of males re-entered. It is possible that female salmon are more sensitive to olfactory cues than are males, as evidenced by reports of decreased stray rates in female salmon (Hard and Heard 1999), and that alterations to the

olfactory environment near spawning grounds could disrupt female navigation more so than male navigation. It is also possible that the tagging and transporting of fish elevated physiological stress, which had a larger impact on females, as we have seen with other studies. Whatever the cause, this is another example that suggests females are more negatively affected than males by changes in migratory conditions.

Though the vast majority of published research on adult freshwater salmon migrations in the Fraser River have focused on sockeye salmon (Johnson et al. 2012), recent studies reveal that other salmon species also display disproportionate female mortality. Teffer et al. (2019) examined survival of adult Fraser River fall-run coho salmon (*O. kisutch*; Chilliwack Hatchery population; Fig. 1) held under cool (10 °C) and warm (15 °C) thermal conditions until they matured. Female mortality was 35% in the warm treatment compared with no male mortality, while all females and males survived the cool treatment. Female mortality in a similar 4-day thermal study involving adult Fraser River fall-run Chinook salmon (*O. tshawytscha*) from the same hatchery (Teffer et al. 2018) was twice that of males when held at cool temperatures (9 °C: 86% versus 37%) and about 30% higher mortality at a warmer temperature (14 °C: 100% versus 71%). Some Chinook salmon adults from the hatchery were transported 40 km downriver, radio-tagged, and released. None of the females survived the return migration to the hatchery despite cool river temperatures (8–12 °C), 76% of the males returned. Thus, like sockeye salmon, female Chinook salmon are more negatively affected by physiological stressors and are less able to survive to natal areas if stressed. The coho salmon and Chinook salmon studies also examined survival after release from gillnet entanglement. Like sockeye salmon, female coho salmon mortality was nearly twice that of males when temperatures were warm. Although Chinook salmon did not show differential sex mortality in the laboratory gillnet study, female mortality was 1.5 times higher than males during river migration following gillnet entanglement. Lastly, this phenomenon is not just restricted to Fraser River populations. A recent study in northern British Columbia on Nass River sockeye salmon found relatively higher female mortality associated with fisheries handling. Fish were captured in marine areas by purse seine and experimentally held in the net for 30–45 min, then brought on board, tagged, and tracked to spawning areas. Females exhibited 52% higher probability of mortality than males (Reid 2020).

### Summary of mortality studies

Male mortality was never observed to be greater than that of females for the 40 situations where male and female survivorship could be contrasted in the 19 Fraser River sockeye salmon studies we reviewed (Fig. 3). On average, females exhibited 2.1 times higher mortality than males (SD 1.38; median 1.85), with mortality three times or greater in six situations and eight times higher in one case (Fig. 3). The type, magnitude, and duration of stressors played important roles in terms of the differences in sex-specific mortality. We demonstrated that laboratory situations can be inherently stressful to wild migrating salmon and that only minor stressors (e.g., confinement or blood sampling) can result in differential mortality between sexes. Field tracking studies have also revealed strong sex-specific mortality patterns, with high temperatures and more invasive stressors (e.g., gillnet entanglement, exhaustive swimming) being additive, and possibly multiplicative, factors. We observed few or only small differences between male and female mortality under extreme and long-duration stressors (e.g., extremely high temperatures). In contrast, stressors that were not immediately lethal or of short to modest duration led to the largest differences between male and female mortality. Field studies (e.g., Martins et al. 2012b) and some of the longer-term lab studies (e.g., Teffer et al. 2017) also revealed that differential female mortality is greatest towards the end of their spawning migration period, suggesting that elevated female mortality may be associated

with aspects of maturation and senescence. Mortality in spawning sockeye is associated with rapid increases in stress responses (i.e., large increases in plasma cortisol; Hruska et al. 2010), an inability to ionoregulate (i.e., large declines in plasma chloride; Jeffries et al. 2011), immunosuppression, and cellular apoptosis (Jeffries et al. 2012b). It is unlikely that any single mechanism can drive differential mortality rates between sexes, but below we review several potential causes that could contribute to this phenomenon.

## Causes of high female mortality

### Energy exhaustion

During the later portions of marine migration and throughout the entire freshwater migration, returning Pacific salmon are no longer feeding and therefore rely entirely on stored energy reserves (Brett 1995). In populations with long, challenging migrations, the amount of energy required to complete the migration and spawn can be high. Some populations of Fraser River sockeye salmon use 91%–96% of their fat reserves between entry into fresh water and the completion of spawning (Crossin et al. 2004). The energetic requirements of females are greater than that of males during this period, because they must devote a larger proportion of their somatic energy to gonads; the gonad mass relative to body mass in mature sockeye salmon can be large: 18% in females versus 3% in males (Crossin et al. 2004). As one example, female Early Stuart sockeye salmon use 20%–30% more energy by the end of their migration than males (Crossin et al. 2004). Females must also retain a greater amount of energy for postmigration activity, as they deplete substantially more energy on spawning grounds than males (Hruska et al. 2010).

Perhaps due to their large energy requirements for gonad development and spawning, females use energy more efficiently while swimming upstream. Electromyogram telemetry in the lower Fraser River found that female sockeye salmon swam slower and used less energy per metre than males, yet they migrated at the same rate (Hinch and Rand 1998). In turbulent, high-velocity reaches, however, energy use is much higher for both sexes, which can lead to excessive energy depletion and elevated in-river mortality (Rand and Hinch 1998). Evidence of an increased reliance by females on burst swimming and anaerobiosis in high-velocity water (Burnett et al. 2014a) suggests that the combination of gonad development and turbulent migratory conditions could easily accelerate energy depletion in females, possibly to the point of energetic exhaustion. Early Stuart sockeye salmon have one of the longest migrations in the Fraser River system (Fig. 1), and these fish have been shown to be at high risk of energy exhaustion prior to spawning ground arrival (Rand et al. 2006). Females typically outnumbered males on spawning grounds from the 1940s until the 1990s. However, in recent years, males have begun outnumbering females (Fig. 2). During this recent period, the lowest percentages of females occurred during years with some of the highest levels of discharge in the Fraser River system (Patterson et al. 2016). This shift in sex ratio on spawning grounds could be influenced by increasing energetic demands due to higher water velocities.

Many of the holding and tracking studies we reviewed that found elevated female mortality were conducted on populations with less strenuous migrations than the Early Stuart populations, and in these cases, females often appeared to have ample energy reserves prior to their death. For example, Crossin et al. (2008) and Nadeau et al. (2010) noted that at the end of their holding experiments, the fish had somatic energy levels well above those at which we have determined death occurs in Fraser River sockeye salmon (i.e., 4 MJ·kg<sup>-1</sup>), which indicates mortality was unlikely to be caused by energy exhaustion. These salmon were from the Weaver Creek population, which has one of the shortest migrations in the Fraser River system (Fig. 1). Accordingly, it is likely that energy exhaustion is not the primary cause of mortality in



populations with less strenuous migrations, but that it may contribute to female-specific mortality in longer distance migrants (e.g., Early Stuart populations).

### Aerobic scope, greedy gonads, and cardiac collapse

Sex-specific differences in cardiorespiratory capacity could generate differential survival between the sexes, particularly under stressful migratory conditions such as high temperatures. A salmon has a finite aerobic capacity (aka aerobic scope), which represents the energy available to do any activity above routine maintenance activities, such as swim upstream, develop gonads, and fight for mates. While cardiorespiratory performance has not been compared across temperatures between sexes in sockeye salmon, Clark et al. (2011) found that male adult pink salmon (*Oncorhynchus gorbuscha*) had higher maximum oxygen consumption rates, aerobic scope, and maximum cardiac output than females across a range of temperatures (8 to 28 °C). In Fraser River sockeye salmon, the relative ventricular mass of mature males is 11%–13% larger than that of females (Sandblom et al. 2009). Larger ventricles are associated with increased maximum stroke volume and cardiac output, as well as a greater ability to generate cardiac pressure (Gamperl and Farrell 2004). Mature female Fraser River sockeye salmon also have routine heart rates that are 21% higher than in males (Sandblom et al. 2009). Higher heart rates and lower relative ventricular mass could lead to decreased cardiac capacity and insufficient scope, particularly at higher temperatures, to complete migration (Eliason et al. 2011). Given that gonads are a greater proportion of body mass in females than in males, females likely divert more blood to this organ during maturation. This type of partitioning of blood flow could further limit female aerobic scope and might explain why female mortality is particularly high towards the end of their upriver migration, as this is when gonads are developing fastest.

With limited aerobic scope, females would have to disproportionately utilize anaerobic metabolism, resulting in elevated plasma H<sup>+</sup> and K<sup>+</sup> (Wood et al. 1983), which can further impair cardiac contractility (Hanson et al. 2006) and could contribute to cardiac collapse. Following anaerobic activity, fish undergo a recovery period during which homeostatic imbalances are restored and high-energy phosphates and oxygen stores are replenished (Scarabello et al. 1992). Excess postexercise oxygen consumption is the collective amount of oxygen required to recover from exercise (Lee et al. 2003). If females exert a greater anaerobic effort in response to a stressor, they would have a greater excess postexercise oxygen consumption and take longer to recover. Delayed recovery could result in increased susceptibility to predation or result in negative carryover effects such as prolonged migration duration and thus elevated mortality in females (e.g., Burnett et al. 2014a).

### Differential stress response

A core component of the stress response in teleost fish is the activation of the hypothalamic–pituitary–interrenal axis (Mommensen et al. 1999), which triggers the release of cortisol and other corticosteroids. Cortisol contributes to the mobilization of energy reserves, the increase in oxygen supply to the tissues, and the maintenance of ionic balance (Pickering 1993), all of which allow the fish to cope with stressors. Plasma cortisol levels increase in response to a wide variety of environmental stressors, and the ubiquity of this response has led to its frequent use as a reliable indicator of stress in salmonids (Pickering 1993). In Pacific salmon, plasma cortisol levels increase throughout the salmon spawning migration, and females have higher base levels than males (Cook et al. 2011). Females also respond more strongly to stress than males do, as evidenced by higher levels of plasma cortisol following exposure to different stressors (e.g., exhaustive exercise — Gale et al. 2011; high temperatures — Jeffries et al. 2012a).

Higher baseline or stress-induced cortisol concentrations in females may contribute to higher mortality for females. Elevated cortisol may have a negative effect on metabolic recovery by playing a role in the regulation of lactate metabolism, a by-product of anaerobiosis. Following exhaustive exercise, metabolic recovery (e.g., plasma lactate, muscle glycogen, blood pH, muscle intracellular pH) was much faster in rainbow trout (*Oncorhynchus mykiss*) that had pharmacologically blocked cortisol levels compared with control trout (Pagnotta et al. 1994). Prolonged cortisol recovery could impact salmon swimming behaviour and cause higher energy use. Moreover, female salmon, with their elevated baseline cortisol levels, may have an impaired response to additional stressors, such that they cannot effectively mobilize additional energy stores or clear waste products. Indeed, prespawn mortality of female pink salmon and migration mortality in sockeye salmon in the Fraser River are associated with elevated baseline and stress-induced cortisol levels (Cook et al. 2011).

### Compromised immune response

Stress and elevated cortisol levels can contribute to mortality through immunosuppression and increased susceptibility to infectious disease (Pickering and Pottinger 1989). For example, captivity stress increased coho salmon mortality when challenged with the pathogen *Vibrio anguillarum* (Salonius and Iwama 1991). Moreover, experimental administration of cortisol replicates the immune suppression seen with stress (Woo et al. 1987), and a direct correlation exists between disease-induced mortality and plasma cortisol levels (Pickering and Pottinger 1989). Androgens such as testosterone are also immunosuppressive (Slater et al. 1995). Salmon may therefore be most susceptible to stress-induced disease towards the end of their migration in association with elevated plasma androgens and cortisol, whose levels in female salmon are naturally much higher than in males at this time of their life history (Hinch et al. 2006). Female salmonids could thus be less resistant to pathogens than are males and consequently suffer higher infection-related mortality because of their elevated cortisol and androgen levels.

Bass et al. (2017) found higher loads of *Flavobacterium psychrophilum* in adult female Chinook salmon during migration in association with the elevated androgen, 17 $\beta$ -estradiol. Also, the gill expression of immune-related gene transcripts was elevated in female sockeye salmon but not in males, pointing to a sex-related influence on immune function (Teffer et al. 2017). Coho salmon also show sex-specific differences in plasma stress indicators and pathogen loads that indicate a weaker defense against infection in females (Teffer et al. 2019). Thus, elevated female sockeye salmon mortality in lab experiments, despite optimal water flow and temperature, could, in part, reflect an impaired immune response and higher pathogen load.

Unfavorable environmental factors clearly exacerbate the effects of stress and immunosuppression on migrating females. Warm water, for example, encourages pathogen proliferation in sockeye salmon (Crossin et al. 2008). *Parvicapsula minibicornis*, which is highly prevalent in migrating adult Fraser River sockeye salmon and whose spores can damage the kidneys and gills, affecting osmoregulation and respiration, develops and spreads faster in higher temperatures (Crossin et al. 2008). Also, high mortality in female coho salmon exposed to gillnetting at high temperatures was attributed to a combination of decreased resilience and enhanced infection intensities (Teffer et al. 2019). Importantly, females and males were equally more resilient to capture stress in cool water temperatures, suggesting the direct additive effect of temperature and stress on immune function and that mortality is more pronounced in females.

### Females in some populations may be more resilient

Our review highlights many examples of the limited capacity of female Pacific salmon to cope with multiple stressors while



demonstrating linkages between energy stores and usage, cardiovascular abilities, hormones, immunity, pathogens, and mortality. These differential sex effects are even evident at the population level, with declining percentages of females on spawning grounds over the past decades for early summer (Early Stuart) and late summer (late-run) sockeye salmon populations, but not in some populations that migrate in midsummer (summer-run populations; Fig. 2). Historically, summer-run populations have had fewer “catastrophic” migration mortality events compared with early summer and late summer populations (Hinch and Martins 2011), which in and of itself suggests greater tolerance to stressors. The Chilko population, a summer-run population, for example, has a unique cardiovascular thermal adaptation: high densities of adrenaline-binding receptors on their heart ventricles ( $\beta$ -adrenoceptors), which can both stimulate and protect cardiac performance and a high capacity to rapidly cycle calcium in the heart (termed “elevated SERCA activity”), enhancing cardiac capacity at high water temperature (Eliason et al. 2011). In general, summer-run populations also have the highest acute thermal tolerance (Eliason et al. 2011), a putative adaptation for coping with the highest encountered migration water temperatures. Thus, it is possible that even with recently changing environmental conditions, the changes were not harsh enough to trigger excessive female mortality in summer-run populations. However, if experimental conditions are sufficiently severe and persistent in laboratory and field studies, female summer-run sockeye salmon still exhibit higher mortality than males (Table A2; Jeffries et al. 2014; Bass et al. 2018b).

### Conservation and management implications

Beyond basic scientific inquiry, understanding the skewed sex ratio on several spawning areas and all the observations we have made from lab and field studies has crucial conservation and management implications. Pacific salmon stocks are important culturally to Canadian First Nations and ecologically as salmon are considered keystone species in many ecosystems. Salmon fishing in British Columbia is a large sector of the economy, supporting >8000 jobs and creating >\$200 million in annual tax revenues; wholesale commercial fishery landings are annually valued at \$100–\$200 million, and the recreational fishery generates nearly \$1 billion in economic impact each year (BCFFS 2013; BCMOA 2017). Despite their importance, Pacific salmon populations in British Columbia have been in decline over the past several decades, which has led to a federal judicial inquiry (Cohen 2012) and the identification of 24 populations as threatened or endangered (COSEWIC 2021).

Nevertheless, fisheries regulators in most jurisdictions, and even the federal agency that manages Pacific salmon in Canada (Fisheries and Oceans Canada, or DFO) do not explicitly consider sex ratios when setting spawning escapement targets (e.g., the desired number of fish to reach spawning grounds to meet management and conservation objectives; Patterson et al. 2016). Given the recent trends highlighted here, managers could benefit from considering objectives that include female-specific targets for spawners. This would require a close look at different tools that could be used by management to achieve sex-specific targets, such as selective fishing or harvest reductions. At present, DFO managers adjust harvest rates during the fishing season based on Fraser River temperature, Fraser River discharge, and river-entry timing to compensate for expected levels of migration mortality for both sexes (Macdonald et al. 2010). Any sex-specific management actions for the Fraser River, if they were to occur, would be best focused on the early- and late-timed runs, which have notable declines in female spawners. It is conceivable that “in-season” harvest decisions could be made that incorporate sex information because DFO can now undertake genetic sex identification as part of their in-season genetic stock

identification program (Ben Sutherland, DFO, personal communication), which is based on tissue samples obtained in test fisheries.

An excellent example of how refining management actions has benefitted female migration survival involves water release at a small dam on a tributary of the Fraser River. Adult Gates Creek sockeye salmon must pass BC Hydro’s Seton River Dam by first locating and ascending a 107 m long vertical-slot fishway, then completing a 50 km migration to spawning areas. Like dams and fish passage structures around the world, waterflow from the fishway entrance operationally involves “attraction flows” intended to draw fish towards the fishway entrance, and this operational protocol has been used for 60 years. However, elevated postpassage mortality was observed in female sockeye salmon (Burnett et al. 2014a, 2014b) when attraction flows had high velocity and turbulence. Exhaustive swimming at the fishway entrance was hypothesized as a cause of the elevated mortality. Experiments conducted in 2014 and 2016 examined migration survival when attraction flows were reduced, creating less turbulence and slower water velocity at the fishway entrance (Burnett et al. 2017; Harrower et al. 2019). This alternative flow release improved rates of fishway passage and subsequent survival to spawning areas for both sexes. Importantly, females benefitted the most (25% increase in females, 10% increase in males; Harrower et al. 2019). That the alternative flow is now operated by BC Hydro during adult salmon runs not only illustrates that basic research can better inform management actions to improve salmon survival, but provides clear empirical evidence that female adult sockeye salmon are more susceptible to some anthropogenic stressors than males.

Given that historically, spawning females outnumbered males, there has been little conservation concern about differential mortality between the sexes. Our findings of decreasing levels of females on spawning grounds in recent years, and the propensity for females to perish at much higher rates than males during coastal, estuarine, and river spawning migrations in the largest salmon producing river in Canada, raises concerns for the long-term sustainability of wild Pacific salmon everywhere. The environmental stressors associated with climate change, in particular thermal issues with migrating adult salmon, are likely to make these phenomena even more pronounced (Dahlke et al. 2020). Several of the Fraser River sockeye salmon populations that we report having changing sex ratios are also ones that are in decline (e.g., Early Stuart populations). Our results suggest that sex ratios on spawning grounds might be a useful indicator of stress on a population, and early observations of a skew towards males might be a “red flag” that a population is heading towards a conservation problem. There are many populations of sockeye salmon in northern British Columbia and Alaska that are not in large decline (Ruggerone and Irvine 2018) as so many are in southern British Columbia (Hyatt et al. 2017), although there is good evidence of reductions in mature size and changes to age structure in many of these northern populations (Oke et al. 2020) indicating strong effects of climate change and increased competition. Trends in sex ratios and information on female mortality should be incorporated into assessment and research on these northern populations particularly as several of them are now experiencing summer high water temperatures causing migration mortality (von Biela et al. 2020). We encourage research into how global change could be affecting sex-specific mortality in other fish species and regions and in particular advocate for a more thorough understanding of the physiological underpinnings of high female mortality.

### Acknowledgements

We thank the scores of research assistants, graduate students, and postdoctoral fellows that have led or contributed to the decades of research that form the basis of this review. In particular we acknowledge senior technician Andrew Lotto, who was been

personally involved in helping to design and conduct nearly every Fraser River study that examined differences between salmon sexes. We thank the numerous First Nation groups and Indigenous fishers for access to their territories and assistance with fish collections. We also thank DFO granting collection permits and for access to the Cultus Lake Laboratory, where most of our lab work was conducted.

## References

- Ano, K.V. 1952. The Babine River salmon escapement in 1951. Fisheries Research Board of Canada. Pacific Progress Report 90. pp. 3–8.
- Arendt, J.D., Reznick, D.N., and López-Sepulcre, A. 2014. Replicated origin of female-biased adult sex ratio in introduced populations of the Trinidadian guppy (*Poecilia reticulata*). *Evolution*, **68**: 2343–2356. doi:10.1111/evo.12445. PMID: 24816221.
- Aresco, M.J. 2005. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. *Biol. Conserv.* **123**: 37–44. doi:10.1016/j.biocon.2004.10.006.
- Arnold, K.E., Adam, A., Orr, K.J., Griffiths, R., and Barber, I. 2003. Sex-specific survival and parasitism in three-spined sticklebacks: seasonal patterns revealed by molecular analysis. *J. Fish Biol.* **63**: 1046–1050. doi:10.1046/j.1095-8649.2003.00195.x.
- Barnaby, J.T. 1944. Fluctuations in abundance of red salmon *Oncorhynchus nerka* (Walbaum) of the Karluk River, Alaska. *US Fish Wildl. Serv. Fish. Bull.* **89**: 237–295.
- Bass, A.L., Hinch, S.G., Teffer, A.K., Patterson, D.A., and Miller, K.S. 2017. A survey of microparasites present in adult migrating chinook salmon (*Oncorhynchus tshawytscha*) in southwestern British Columbia determined by high-throughput quantitative polymerase chain reaction. *J. Fish Dis.* **40**: 453–477. doi:10.1111/jfd.12607.
- Bass, A.L., Hinch, S.G., Casselman, M.T., Bett, N.N., Burnett, N.J., Middleton, C.T., and Patterson, D.A. 2018a. Visible gill-net injuries predict migration and spawning failure in adult sockeye salmon. *Trans. Am. Fish. Soc.* **147**: 1085–1099. doi:10.1002/tafs.10103.
- Bass, A.L., Hinch, S.G., Patterson, D.A., Cooke, S.J., and Farrell, A.P. 2018b. Location-specific 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. doi:10.1139/cjfas-2017-0474.
- BCFFS. 2013. Sport Fishing Economic Impact Report. British Columbia Freshwater Fisheries Society. Available from [http://www.gofishbc.com/PDFs/Footer/2013\\_bc\\_freshwater\\_sport\\_fishing\\_economic\\_impact\\_r.aspx](http://www.gofishbc.com/PDFs/Footer/2013_bc_freshwater_sport_fishing_economic_impact_r.aspx).
- BCMOA. 2017. British Columbia Seafood Industry Year in Review, 2016. British Columbia Ministry of Agriculture. Available from <http://www2.gov.bc.ca/gov/content/industry/agriculture-seafood/statistics/industry-and-sector-profiles>.
- Beacham, T.D., Lapointe, M., Candy, J.R., McIntosh, B., Macconnachie, C., Tabata, A., et al. 2004. Stock identification of Fraser River sockeye salmon using microsatellites and major histocompatibility complex variation. *Trans. Am. Fish. Soc.* **133**: 1117–1137. doi:10.1577/I04-001.1.
- Biro, P.A., Post, J.R., and Parkinson, E.A. 2003. From individuals to populations: risk-taking by prey fish mediates mortality in whole-system experiments. *Ecology*, **84**: 2419–2431. doi:10.1890/02-0416.
- Brett, J.R. 1995. Energetics. In *Physiological Ecology of Pacific Salmon*. Edited by C. Groot, L. Margolis, and C. Clarke. UBC Press, Vancouver, Canada. pp. 1–68.
- Britton, R.H., and Moser, M.E. 1982. Size specific predation by herons and its effect on the sex-ratio of natural populations of the mosquitofish *Gambusia affinis* Baird and Girard. *Oecologia*, **53**: 146–151. doi:10.1007/BF00545657. PMID: 28311103.
- Burgner, R.L. 1991. Life history of sockeye salmon *Oncorhynchus nerka*. In *Pacific Salmon Life Histories*. Edited by C. and Groot and C. Margolis. UBC Press, Vancouver, Canada. pp. 3–117.
- Burnett, N.J., Hinch, S.G., Donaldson, M.R., Furey, N.B., Patterson, D.A., Roscoe, D.W., and Cooke, S.J. 2014a. Alterations to dam-spill discharge influence sex-specific activity, behaviour and passage success of migrating adult sockeye salmon. *Ecology*, **7**: 1094–1104.
- Burnett, N.J., Hinch, S.G., Braun, D.C., Casselman, M.T., Middleton, C.T., Wilson, S.M., and Cooke, S.J. 2014b. Burst swimming in areas of high flow: delayed consequences of anaerobiosis in wild adult sockeye salmon. *Physiol. Biochem. Zool.* **87**: 587–598.
- Burnett, N.J., Hinch, S.G., Bett, N.N., Braun, D.C., Casselman, M.T., Cooke, S.J., et al. 2017. Reducing carryover effects on the migration and spawning success of sockeye salmon through a management experiment of dam flows. *River Res. Appl.* **33**: 3–15. doi:10.1002/rra.3051.
- Christe, P., Keller, L., and Roulin, A. 2006. The predation cost of being a male: implications for sex-specific rates of ageing. *Oikos*, **114**: 381–394. doi:10.1111/j.2006.0030-1299.15130.x.
- Clark, T.D., Jeffries, K.M., Hinch, S.G., and Farrell, A.P. 2011. Exceptional aerobic scope and cardiovascular performance of pink salmon (*Oncorhynchus gorbuscha*) may underlie resilience in a warming climate. *J. Exp. Biol.* **214**: 3074–3081. doi:10.1242/jeb.060517.
- Clutton-Brock, T.H., and Iason, G.R. 1986. Sex ratio variation in mammals. *Q. Rev. Biol.* **61**: 339–374. doi:10.1086/415033.
- Cohen, B.I. 2012. The uncertain future of Fraser River sockeye: v. 1. The sockeye fishery. In *Cohen Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River — final report* [by] Bruce I. Cohen, commissioner, [for the] Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River. Government of Canada Privy Council, Ottawa, Ont.
- Connors, B., Malick, M.J., Ruggerone, G.T., Rand, P., Adkison, M., Irvine, J.R., et al. 2020. Climate and competition influence sockeye salmon population dynamics across the Northeast Pacific Ocean. *Can. J. Fish. Aquat. Sci.* **77**(6): 943–949. doi:10.1139/cjfas-2019-0422.
- Cook, K.V., McConnachie, S.H., Gilmour, K.M., Hinch, S.G., and Cooke, S.J. 2011. Fitness and behavioral correlates of pre-stress and stress-induced plasma cortisol titers in pink salmon (*Oncorhynchus gorbuscha*) upon arrival at spawning grounds. *Horm. Behav.* **60**: 489–497. doi:10.1016/j.yhbeh.2011.07.017. PMID: 21839080.
- Cooke, S.J., and Hinch, S.G. 2013. Improving the reliability of fishway attraction and passage efficiency estimates to inform fishway engineering, science, and practice. *Ecol. Eng.* **58**: 123–132. doi:10.1016/j.ecoleng.2013.06.005.
- COSEWIC. 2021. Committee on the Status of Endangered Wildlife in Canada. Available from <https://species-registry.canada.ca/index-en.html#/documents?documentTypeId=18&sortBy=documentTypeSort&sortDirection=asc&pageSize=10>.
- Crossin, G.T., Hinch, S.G., Farrell, A.P., Higgs, D.A., Lotto, A.G., Oakes, J.D., and Healey, M.C. 2004. Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *J. Fish Biol.* **65**: 788–810. doi:10.1111/j.0022-1112.2004.00486.x.
- Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Lotto, A.G., Patterson, D.A., et al. 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migrations. *Can. J. Zool.* **86**(2): 127–140. doi:10.1139/Z07-122.
- Dahlke, F.T., Wohlrab, S., Butzin, M., and Pörtner, H.O. 2020. Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, **369**: 65–70. doi:10.1126/science.aaz3658. PMID: 32631888.
- DFO. 2001. A policy for selective fishing in Canada's Pacific fisheries. Fisheries and Oceans Canada. Available from <http://www.dfo-mpo.gc.ca/Library/252358.pdf>.
- DFO. 2019. Environmental Watch Program. Fisheries and Oceans Canada. Available from <https://www.pac.dfo-mpo.gc.ca/science/habitat/frw-rfo/index-eng.html>.
- Donald, P.F. 2007. Adult sex ratios in wild bird populations. *Ibis*, **149**: 671–692. doi:10.1111/j.1474-919X.2007.00724.x.
- Drenner, S.M., Harrower, W.L., Casselman, M.T., Bett, N.N., Bass, A.L., Middleton, C.T., and Hinch, S.G. 2018. Whole-river manipulation of olfactory cues affects upstream migration of sockeye salmon. *Fish. Manage. Ecol.* **25**: 488–500.
- Eiler, J.H., Evans, A.N., and Schreck, C.B. 2015. Migratory patterns of wild Chinook salmon *Oncorhynchus tshawytscha* returning to a large, free-flowing river basin. *PLoS ONE*, **10**: e0123127. doi:10.1371/journal.pone.0123127. PMID: 25919286.
- Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., et al. 2011. Differences in thermal tolerance among sockeye salmon populations. *Science*, **332**: 109–112. doi:10.1126/science.1199158. PMID: 21454790.
- Foerster, R.E. 1954. Sex ratios in sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Can.* **11**: 988–997. doi:10.1139/f54-056.
- Gale, M.K., Hinch, S.G., Eliason, E.J., Cooke, S.J., and Patterson, D.A. 2011. Physiological impairment of adult sockeye salmon in fresh water after simulated capture-and-release across a range of temperatures. *Fish. Res.* **112**: 85–95. doi:10.1016/j.fishres.2011.08.014.
- Gale, M.K., Hinch, S.G., Cooke, S.J., Donaldson, M.R., Eliason, E.J., Jeffries, K.M., Martins, E.G., and Patterson, D.A. 2014. Observable impairments predict mortality of captured and released sockeye salmon at various temperatures. *Conserv. Physiol.* **2**(1): cou029.
- Gamperl, A.K., and Farrell, A.P. 2004. Cardiac plasticity in fishes: environmental influences and intraspecific differences. *J. Exp. Biol.* **207**: 2539–2550. doi:10.1242/jeb.01057.
- Gilhouse, P. 1990. Prespawning mortalities of sockeye salmon in the Fraser River system and possible causal factors. IPSC Bulletin XXVI. International Pacific Salmon Fisheries Commission, Vancouver, B.C., Canada.
- Hanson, L.M., Obradovich, S., Mouniargi, J., and Farrell, A.P. 2006. The role of adrenergic stimulation in maintaining maximum cardiac performance in rainbow trout (*Oncorhynchus mykiss*) during hypoxia, hyperkalemia and acidosis at 10°C. *J. Exp. Biol.* **209**: 2442–2451. doi:10.1242/jeb.02237.
- Hard, J.J., and Heard, W.R. 1999. Analysis of straying variation in Alaskan hatchery Chinook salmon (*Oncorhynchus tshawytscha*) following transplantation. *Can. J. Fish. Aquat. Sci.* **56**(4): 578–589. doi:10.1139/f98-199.
- Hardy, J.C.W. 2002. Sex ratios: concepts and research methods. Cambridge University Press, Cambridge.
- Harrower, W.L., Bett, N.N., and Hinch, S.G. 2019. BRGMON-14: Effectiveness of Cayoosh Flow Dilution, Dam Operation, and Fishway Passage on Delay and Survival of Upstream Migration of Salmon in the Seton-Anderson Watershed. Prepared for St'at'imc Eco-Resources Ltd. and BC Hydro. The University of British Columbia, Vancouver, B.C.
- Hasler, A.D., and Scholz, A.T. 1983. Olfactory imprinting and homing in Salmon. Springer-Verlag, New York.



- Hinch, S.G., and Martins, E.G. 2011. A review of potential climate change effects on survival of Fraser River sockeye salmon and analysis of inter-annual trends in en route loss and pre-spawn mortality. *Cohen Commission Technical Report*. 9. The Cohen Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River, Vancouver, B.C.
- Hinch, S.G., and Rand, P.S. 1998. Swim speeds and energy use of river migrating adult sockeye salmon: role of local environment and fish characteristics. *Can. J. Fish. Aquat. Sci.* **55**(8): 1821–1831. doi:10.1139/f98-067.
- Hinch, S.G., Cooke, S.J., Farrell, A.P., Miller, K.M., Lapointe, M., and 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**: 576–599. doi:10.1111/j.1095-8649.2012.03360.x.
- Hinch, S.G., Cooke, S.J., Healey, M.C., and Farrell, A.P. 2006. Behavioural physiology of fish migrations: salmon as a model approach. In *Fish Physiology Volume 24: Behaviour and Physiology of Fish*. Edited by K. Sloman, S. Balshine, and R. Wilson. Elsevier Press. pp. 239–295.
- Holtby, L.B., and Healey, M.C. 1990. Sex-specific life history tactics and risk-taking in coho salmon. *Ecology*, **71**: 678–690. doi:10.2307/1940322.
- Hruska, K.A., Hinch, S.G., Healey, M.C., Patterson, D.A., Larsson, S., and Farrell, A.P. 2010. Influences of sexual status and behavior on physiological changes among individual adult sockeye salmon during rapid senescence. *Physiol. Biochem. Zool.* **83**: 663–676. doi:10.1086/652411. PMID:20482369.
- Hyatt, K.D., Stockwell, M.M., Ogden, A., and Stiff, H. 2017. Sockeye Salmon indicator stocks—Regional overview of trends, 2016 returns, and 2017–2018 outlook. In *State of the Physical, Biological and Selected Fishery Resources of Pacific Canadian Marine Ecosystems in 2016*. Edited by P.C. Chandler, S.A. King, and J. Boldt. *Can. Tech. Rep. Fish. Aquat. Sci.*
- Jeffries, K.M., Hinch, S.G., Donaldson, M.R., Gale, M.K., Burt, J.M., Thompson, L.A., et al. 2011. Temporal changes in blood variables during final maturation and senescence in male sockeye salmon *Oncorhynchus nerka*: reduced osmoregulatory ability can predict mortality. *J. Fish Biol.* **79**: 449–465. doi:10.1111/j.1095-8649.2011.03042.x.
- Jeffries, K.M., Hinch, S.G., Martins, E.G., Clark, T.D., Lotto, A.G., Patterson, D.A., et al. 2012a. Sex and proximity to reproductive maturity influence the survival, final maturation, and blood physiology of Pacific salmon when exposed to high temperature during a simulated migration. *Physiol. Biochem. Zool.* **85**: 62–73.
- Jeffries, K.M., Hinch, S.G., Sierocinski, T., Clark, T.D., Eliason, E.J., Donaldson, M.R., et al. 2012b. Consequences of high temperatures and premature mortality on the transcriptome and blood physiology of wild adult sockeye salmon (*Oncorhynchus nerka*). *Ecol. Evol.* **2**: 1747–1764. doi:10.1002/ece3.274. PMID:22957178.
- Jeffries, K.M., Hinch, S.G., Sierocinski, T., Pavlidis, P., and Miller, K.M. 2014. Transcriptomic responses to high water temperature in two species of Pacific salmon. *Evol. Appl.* **7**: 286–300.
- Johnson, J.E., Patterson, D.A., Martins, E.G., Cooke, S.J., and Hinch, S.G. 2012. Quantitative methods for analysing cumulative effects on fish migration success: a review. *J. Fish Biol.* **81**: 600–631. doi:10.1111/j.1095-8649.2012.03369.x.
- Jonsson, N., Jonsson, B., and Hansen, L.P. 1991. Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). *J. Fish Biol.* **39**: 739–744. doi:10.1111/j.1095-8649.1991.tb04403.x.
- Keefer, M.L., and Caudill, C.C. 2014. Homing and straying by anadromous salmonids: A review of mechanisms and rates. *Rev. Fish Biol. Fish.* **24**: 333–368. doi:10.1007/s11160-013-9334-6.
- Keefer, M.L., Peery, C.A., and Heinrich, M.J. 2018. Temperature-mediated en route migration mortality and travel rates of endangered Snake River sockeye salmon. *Ecol. Freshw. Fish.* **17**: 136–145.
- Kendall, N.W., and Quinn, T.P. 2013. Size-selective fishing affects sex ratios and the opportunity for sexual selection in Alaskan sockeye salmon *Oncorhynchus nerka*. *Oikos*, **122**: 411–420. doi:10.1111/j.1600-0706.2012.20319.x.
- Lee, C.G., Farrell, A.P., Lotto, A., Hinch, S.G., and Healey, M.C. 2003. Excess post-exercise oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon following critical speed swimming. *J. Exp. Biol.* **206**: 3253–3260. doi:10.1242/jeb.00548.
- Lewis, B., Grant, W.S., Brenner, R.E., and Hamazaki, T. 2015. Changes in size and age of Chinook salmon *Oncorhynchus tshawytscha* returning to Alaska. *PLoS ONE*, **10**(6): e0130184. doi:10.1371/journal.pone.0130184. PMID:26090990.
- Lovich, J.E., and Gibbons, J.W. 1990. Age at maturity influences adult sex ratio in the turtle *Malaclemys terrapin*. *Oikos*, **59**: 126–134. doi:10.2307/3545132.
- Macdonald, J.S., Patterson, D.A., Hague, M.J., and 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**: 768–782. doi:10.1577/T08-223.1.
- Martins, E.G., Hinch, S.G., Patterson, D.A., Hague, M.J., Cooke, S.J., Miller, K.M., et al. 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. doi:10.1111/j.1365-2486.2010.02241.x.
- Martins, E.G., Hinch, S.G., Cooke, S.J., and Patterson, D.A. 2012a. Climate effects on growth, phenology, and survival of sockeye salmon (*Oncorhynchus nerka*): a synthesis of the current state of knowledge and future research directions. *Rev. Fish Biol. Fish.* **22**: 887–914. doi:10.1007/s11160-012-9271-9.
- Martins, E.G., Hinch, S.G., Patterson, D.A., Hague, M.J., Cooke, S.J., Miller, K.M., et al. 2012b. High river temperature reduces survival of sockeye salmon approaching spawning grounds and exacerbates female mortality. *Can. J. Fish. Aquat. Sci.* **69**(2): 330–342. doi:10.1139/f2011-154.
- McKellar, A.E., Turcotte, M.M., and Hendry, A.P. 2009. Environmental factors influencing adult sex ratio in Trinidadian guppies. *Oecologia*, **159**: 735–745. doi:10.1007/s00442-008-1257-x. PMID:19132402.
- McMaster, M., Munkittrick, K., and Van Der Kraak, G. 1992. Protocol for measuring circulating levels of gonadal sex steroids in fish. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1836.
- Mehranvar, L., Healey, M.C., Farrell, A.P., and Hinch, S.G. 2004. Social versus genetic measures of reproductive success in sockeye salmon, *Oncorhynchus nerka*. *Evol. Ecol. Res.* **6**: 1167–1181.
- METABASE Explorer. 2019. The Marine Ecological Time Series database. Available from <https://www.st.nmfs.noaa.gov/copepod/time-series/ca-50901/>.
- Miller, K.M., Li, S., Kaukinen, K.H., Ginther, N., Hammill, E., Curtis, J.M.R., et al. 2011. Genomic signatures predict migration and spawning failure in wild Canadian salmon. *Science*, **331**: 214–217. doi:10.1126/science.1196901. PMID:21233388.
- Mommsen, T.P., Vijayan, M.M., and Moon, T.W. 1999. Cortisol in teleosts: dynamics, mechanisms of action, and metabolic regulation. *Rev. Fish Biol. Fish.* **9**: 211–268. doi:10.1023/A:1008924418720.
- Nadeau, P. 2007. Parental contributions to the early life history traits of juvenile sockeye salmon (*Oncorhynchus nerka*): the roles of spawner identity and migratory experience. M.Sc. thesis. The University of British Columbia, Vancouver, B.C.
- Nadeau, P.S., Hinch, S.G., Hruska, K.A., Pon, L.B., and Patterson, D.A. 2010. The effects of experimental energy depletion on the physiological condition and survival of adult sockeye salmon (*Oncorhynchus nerka*) during spawning migration. *Environ. Biol. Fishes*, **88**: 241–251.
- Oke, K.B., Cunningham, C.J., Westley, P.A.H., Baskett, M.L., Carlson, S.M., Clark, J., et al. 2020. Recent declines in salmon body size impact ecosystems and fisheries. *Nat. Commun.* **11**: 4155. doi:10.1038/s41467-020-17726-z. PMID:32814776.
- Olsen, J.B., Miller, S.J., Harper, K., Nagler, J.J., and Wenburg, J.K. 2006. Contrasting sex ratios in juvenile and adult chinook salmon *Oncorhynchus tshawytscha* (Walbaum) from southwest Alaska: sex reversal or differential survival? *J. Fish Biol.* **69**: 140–144. doi:10.1111/j.1095-8649.2006.01119.x.
- Pagnotta, A., Brooks, L., and Milligan, L. 1994. The potential regulatory roles of cortisol in recovery from exhaustive exercise in rainbow trout. *Can. J. Zool.* **72**(12): 2136–2146. doi:10.1139/z94-286.
- Patterson, D.A., Macdonald, J.S., Hinch, S.G., Healey, M.C., and Farrell, A.P. 2004. The effect of exercise and captivity on energy partitioning, reproductive maturation, and fertilization success in adult sockeye salmon. *J. Fish Biol.* **64**: 1–21.
- Patterson, D.A., Cooke, S.J., Hinch, S.G., Robinson, K.A., Young, N., Farrell, A.P., and 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*). *Conserv. Physiol.* **4**(1): cow026. doi:10.1093/conphys/cow026. PMID:27928508.
- Pettersson, L.B., Ramnarine, I.W., Becher, S.A., Mahabir, R., and Magurran, A.E. 2004. Sex ratio dynamics and fluctuating selection pressures in natural populations of the Trinidadian guppy, *Poecilia reticulata*. *Behav. Ecol. Sociobiol.* **55**: 461–468. doi:10.1007/s00265-003-0727-8.
- Pickering, A.D. 1993. Endocrine-induced pathology in stressed salmonid fish. *Fish. Res.* **17**: 35–50.
- Pickering, A.D., and Pottinger, T.G. 1989. Stress responses and disease resistance in salmonid fish: Effects of chronic elevation of plasma cortisol. *Fish Physiol. Biochem.* **7**: 253–258. doi:10.1007/BF00004714.
- Rand, P.S., and Hinch, S.G. 1998. Swim speeds and energy use of river migrating adult sockeye salmon: simulating metabolic power and assessing risk of energy depletion. *Can. J. Fish. Aquat. Sci.* **55**(8): 1832–1841. doi:10.1139/f98-068.
- Rand, P.S., Hinch, S.G., Morrison, J., Foreman, M.G.G., MacNutt, M.J., Macdonald, J.S., et al. 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**: 655–667. doi:10.1577/T05-023.1.
- Reichard, M., Polacik, M., Blažek, R., and Vrtilek, M. 2014. Female bias in the adult sex ratio of African annual fishes: interspecific differences, seasonal trends and environmental predictors. *Environ. Ecol.* **28**: 1105–1120.
- Reid, A.L. 2020. Fish–People–Place: interweaving knowledges to elucidate Pacific salmon fate. Ph.D. dissertation. Carleton University, Ottawa Ont.
- Ricker, W.E. 1987. Effects of the fishery and of obstacles to migration on the abundance of Fraser River sockeye salmon (*Oncorhynchus nerka*). *Canadian Technical Report of Fisheries and Aquatic Sciences* 1522.
- Robinson, K.A., Hinch, S.G., Gale, M.K., Clark, T.D., Wilson, S.M., Donaldson, M.R., et al. 2013. Effects of post-capture ventilation assistance and elevated water temperature on sockeye salmon in a simulated capture-and-release experiment. *Conserv. Physiol.* doi:10.1093/conphys/cot015.
- Robinson, K.A., Hinch, S.G., Raby, G.D., Donaldson, M.R., Robichaud, D., Patterson, D.A., and Cooke, S.J. 2015. Influence of post-capture ventilation assistance on migration success of adult sockeye salmon following capture and release. *Trans. Am. Fish. Soc.* **144**: 693–704.
- Rodd, F.H., and Reznick, D.N. 1997. Variation in the demography of guppy populations: the importance of predation and life histories. *Ecology*, **78**: 405–418. doi:10.1890/0012-9658(1997)078[0405:VTIDOC]2.0.CO;2. doi:10.2307/2266017.
- Roscoe, D.W., and Hinch, S.G. 2010. Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. *Fish. Fish.* **11**: 12–33. doi:10.1111/j.1467-2979.2009.00333.x.



- Roscoe, D.W., Hinch, S.G., Cooke, S.J., and Patterson, D.A. 2011. Fishway passage and post-passage mortality of up-river migrating sockeye salmon in the Seton River, British Columbia. *River Res. Appl.* **27**: 693–705. doi:10.1002/rra.1384.
- Ruggerone, G.T., and Irvine, J.R. 2018. Numbers and biomass of natural- and hatchery-origin pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean, 1925–2015. *Mar. Coast. Fish.* **10**: 152–168. doi:10.1002/mcf2.10023.
- Salonius, K., and Iwama, G.K. 1991. The effect of stress on the immune function of wild and hatchery coho salmon juveniles. *Bull. Aquacul. Assoc. Can.* **91**: 47–49.
- Sandblom, E., Clark, T.D., Hinch, S.G., and Farrell, A.P. 2009. Sex-specific differences in cardiac control and hematology of sockeye salmon (*Oncorhynchus nerka*) approaching their spawning grounds. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **297**: R1136–R1143. doi:10.1152/ajpregu.00363.2009. PMID:19675278.
- Scarabello, M., Heigenhauser, G.J., and Wood, C.M. 1992. Gas exchange, metabolite status and excess post-exercise oxygen consumption after repetitive bouts of exhaustive exercise in juvenile rainbow trout. *J. Exp. Biol.* **167**: 155–169.
- Slater, C.H., Fitzpatrick, M.S., and Schreck, C.B. 1995. Characterization of an androgen receptor in salmonid lymphocytes: possible link to androgen-induced immunosuppression. *Gen. Comp. Endocrinol.* **100**: 218–225. doi:10.1006/gcen.1995.1151.
- Spidle, A.P., Puinn, T.P., and Bentzen, P. 1998. Sex-biased marine survival and growth in a population of coho salmon. *J. Fish Biol.* **52**: 907–915. doi:10.1111/j.1095-8649.1998.tb00591.x.
- Stoks, R. 2001. What causes male-biased sex ratios in mature damselfly populations? *Ecol. Entomol.* **26**: 188–197. doi:10.1046/j.1365-2311.2001.00303.x.
- Székely, T., Liker, A., Freckleton, R.P., Fichtel, C., and Kappeler, P.M. 2014. Sex-biased survival predicts adult sex ratio variation in wild birds. *Proc. Biol. Sci.* **281**: 20140342. doi:10.1098/rspb.2014.0342. PMID:24966308.
- Tamate, T., and Maekawa, K. 2004. Female-biased mortality rate and sexual size dimorphism of migratory masu salmon, *Oncorhynchus masou*. *Ecol. Freshwater Fish.* **13**: 96–103. doi:10.1111/j.1600-0633.2004.00043.x.
- Teffer, A.K., Hinch, S.G., Miller, K.S., Patterson, D.A., Farrell, A.P., Cooke, S.J., et al. 2017. Capture severity, infectious disease processes, and sex influence post-release mortality of sockeye salmon bycatch. *Conserv. Physiol.* **5**(1): cox017. doi:10.1093/conphys/cox017.
- Teffer, A.K., Bass, A.L., Miller, K.S., Patterson, D.A., Juanes, F., and Hinch, S.G. 2018. Infections, fisheries capture, temperature, and host responses: multi-stressor influences on survival and behavior of adult Chinook salmon. *Can. J. Fish. Aquat. Sci.* **75**(11): 2069–2083. doi:10.1139/cjfas-2017-0491.
- Teffer, A.K., Hinch, S.G., Miller, K.M., Jeffries, K.M., Patterson, D.A., Cooke, S.J., et al. 2019. Sex-specific effects of thermal and fisheries stressors on pathogen development and early mortality of adult coho salmon (*Oncorhynchus kisutch*) in freshwater. *Physiol. Biochem. Zool.* **92**(5): 505–529. doi:10.1086/705125.
- von Biela, V.R., Bowen, L., McCormick, S.D., Carey, M.P., Donnelly, D.S., Waters, S., et al. 2020. Evidence of prevalent heat stress in Yukon River Chinook salmon. *Can. J. Fish. Aquat. Sci.* **77**(12): 1878–1892. doi:10.1139/cjfas-2020-0209.
- Whitney, C.K., Hinch, S.G., and Patterson, D.A. 2014. Population origin and water temperature affect development timing in embryonic sockeye salmon. *Trans. Am. Fish. Soc.* **143**: 1316–1329. doi:10.1080/00028487.2014.935481.
- Woo, P.T.K., Leatherland, J.F., and Lee, M.S. 1987. *Cryptobia salmositica*: cortisol increases the susceptibility of *Salmo gairdneri* Richardson to experimental cryptobiosis. *J. Fish. Dis.* **10**: 75–83.
- Wilson, E.O. 1975. *Sociobiology: the new synthesis*. Harvard University Press, Cambridge, Mass.
- Wood, C.M., Turner, J.D., and Graham, M.S. 1983. Why do fish die after severe exercise? *J. Fish Biol.* **22**: 189–201. doi:10.1111/j.1095-8649.1983.tb04739.x.

Appendix Tables A1 and A2 appear on the following pages.

## Appendix A

**Table A1.** Studies from the Fraser River watershed that examined sex-specific differences in adult sockeye salmon survival (Nos. 1–19) and in adult Chinook and coho salmon (Nos. 20–22).

Study No.	Citation
1	Patterson, D.A., Macdonald, J.S., Hinch, S.G., Healey, M.C., and Farrell, A.P. 2004. The effect of exercise and captivity on energy partitioning, reproductive maturation, and fertilization success in adult sockeye salmon. <i>J. Fish Biol.</i> <b>64</b> : 1–21.
2, 3	Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Lotto, A.G., Patterson, D.A., Jones, S.R.M., Leggatt, R.A., Mathes, M.T., Shrimpton, J.M., Van Der Kraak, G., and Farrell, A.P. 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migrations. <i>Can. J. Zool.</i> <b>86</b> (2): 127–140.
4	Nadeau, P.S., Hinch, S.G., Hruska, K.A., Pon, L.B., and Patterson, D.A. 2010. The effects of experimental energy depletion on the physiological condition and survival of adult sockeye salmon ( <i>Oncorhynchus nerka</i> ) during spawning migration. <i>Environ. Biol. Fishes</i> , <b>88</b> : 241–251.
5	Roscoe, D.W., Hinch, S.G., Cooke, S.J., and Patterson, D.A. 2011. Fishway passage and post-passage mortality of up-river migrating sockeye salmon in the Seton River, British Columbia. <i>River Res. Appl.</i> <b>27</b> : 693–705.
6	Martins, E.G., Hinch, S.G., Patterson, D.A., Hague, M.J., Cooke, S.J., Miller, K.M., Robichaud, D., English, K.K., and Farrell, A.P. 2012b. High river temperature reduces survival of sockeye salmon approaching spawning grounds and exacerbates female mortality. <i>Can. J. Fish. Aquat. Sci.</i> <b>69</b> (2): 330–342.
7	Jeffries, K.M., Hinch, S.G., Martins, E.G., Clark, T.D., Lotto, A.G., Patterson, D.A., Cooke, S.J., Farrell, A.P., and Miller, K.M. 2012a. Sex and proximity to reproductive maturity influence the survival, final maturation, and blood physiology of Pacific salmon when exposed to high temperature during a simulated migration. <i>Physiol. Biochem. Zool.</i> <b>85</b> : 62–73.
8	Robinson, K.A., Hinch, S.G., Gale, M.K., Clark, T.D., Wilson, S.M., Donaldson, M.R., Farrell, A.P., Cooke, S.J., and Patterson, D.A. 2013. Effects of post-capture ventilation assistance and elevated water temperature on sockeye salmon in a simulated capture-and-release experiment. <i>Conserv. Physiol.</i> <b>1</b> (1): cot015.
9	Burnett, N.J., Hinch, S.G., Donaldson, M.R., Furey, N.B., Patterson, D.A., Roscoe, D.W., and Cooke, S.J. 2014a. Alterations to dam-spill discharge influence sex-specific activity, behaviour and passage success of migrating adult sockeye salmon. <i>Ecohydrology</i> , <b>7</b> : 1094–1104.
10	Burnett, N.J., Hinch, S.G., Braun, D.C., Casselman, M.T., Middleton, C.T., Wilson, S.M., and Cooke, S.J. 2014b. Burst swimming in areas of high flow: delayed consequences of anaerobiosis in wild adult sockeye salmon. <i>Physiol. Biochem. Zool.</i> <b>87</b> : 587–598.
11, 12	Jeffries, K.M., Hinch, S.G., Sierocinski, T., Pavlidis, P., and Miller, K.M. 2014. Transcriptomic responses to high water temperature in two species of Pacific salmon. <i>Evol. Appl.</i> <b>7</b> : 286–300.
13	Gale, M.K., Hinch, S.G., Cooke, S.J., Donaldson, M.R., Eliason, E.J., Jeffries, K.M., Martins, E.G., and Patterson, D.A. 2014. Observable impairments predict mortality of captured and released sockeye salmon at various temperatures. <i>Conserv. Physiol.</i> <b>2</b> (1): cou029.
14	Robinson, K.A., Hinch, S.G., Raby, G.D., Donaldson, M.R., Robichaud, D., Patterson, D.A., and Cooke, S.J. 2015. Influence of post-capture ventilation assistance on migration success of adult sockeye salmon following capture and release. <i>Trans. Am. Fish. Soc.</i> <b>144</b> : 693–704.
15	Teffer, A.K., Hinch, S.G., Miller, K.S., Patterson, D.A., Farrell, A.P., Cooke, S.J., Bass, A.L., Szekeres, P., and Juanes, F. 2017. Capture severity, infectious disease processes, and sex influence post-release mortality of sockeye salmon bycatch. <i>Conserv. Physiol.</i> <b>5</b> (1): cox017.
16, 17	Bass, A.L., Hinch, S.G., Patterson, D.A., Cooke, S.J., and Farrell, A.P. 2018b. Location-specific consequences of beach seine and gillnet capture on upriver-migrating sockeye salmon migration behavior and fate. <i>Can. J. Fish. Aquat. Sci.</i> <b>75</b> (11): 2011–2023.
18	Harrower, W.L., Bett, N.N., and Hinch, S.G. 2019. BRGMON-14: Effectiveness of Cayoosh Flow Dilution, Dam Operation, and Fishway Passage on Delay and Survival of Upstream Migration of Salmon in the Seton–Anderson Watershed. Prepared for St'at'imc Eco-Resources Ltd. and BC Hydro. The University of British Columbia, Vancouver, B.C.
19	Drenner, S.M., Harrower, W.L., Casselman, M.T., Bett, N.N., Bass, A.L., Middleton, C.T., and Hinch, S.G. 2018. Whole-river manipulation of olfactory cues affects upstream migration of sockeye salmon. <i>Fish. Manage. Ecol.</i> <b>25</b> : 488–500.
20, 21	Teffer, A.K., Bass, A.L., Miller, K.S., Patterson, D.A., Juanes, F., and Hinch, S.G. 2018. Infections, fisheries capture, temperature, and host responses: multistressor influences on survival and behavior of adult Chinook salmon. <i>Can. J. Fish. Aquat. Sci.</i> <b>75</b> (11): 2069–2083.
22	Teffer, A.K., Hinch, S.G., Miller, K.M., Jeffries, K.M., Patterson, D.A., Cooke, S.J., Farrell, A.P., Kaukinen, K., Li, S., and Juanes, F. 2019. Sex-specific effects of thermal and fisheries stressors on pathogen development and early mortality of adult coho salmon ( <i>Oncorhynchus kisutch</i> ) in freshwater. <i>Physiol. Biochem. Zool.</i> <b>92</b> (5): 505–529.

**Note:** Study number corresponds to study details in Table A2 and to the geographic location of the study population natal area in Fig. 1.

**Table A2.** Summary of results from studies on adult Fraser River salmon that examined sex-specific mortality.

Study No.	Population (or run timing and group)	Study year	Lab or field	Study design and citation	Primary stressor(s)	Treatment No.	% mortality (female)	% mortality (male)	Relative magnitude of female mortality (female/male)
1	Early Stuart	1999	Lab	Adults captured in lower Fraser River by dip net and held in cool water tanks for 25 days (Patterson et al. 2004)	Captivity	1	50%	25%	2.0
2	Weaver Creek	2004	Lab	Adults captured in Harrison River, held in 18 or 10 °C tanks for 21 days (Crossin et al. 2008)	Temperature, captivity	2 3	10 °C: 24% 18 °C: 44%	10 °C: 14% 18 °C: 22%	10 °C: 1.7 18 °C: 2.0
3	Weaver Creek	2004	Field	Thermally treated adults from study 2 released in Fraser River, gastrically tagged with radio transmitters, tracked to spawning grounds (Crossin et al. 2008)	Temperature	4 5	10 °C: 30% 18 °C: 90%	10 °C: 30% 18 °C: 45%	10 °C: 1 18 °C: 2.0
4	Weaver Creek	2005, 2006	Lab	Adults held in cool water raceways for 18 days (Nadeau et al. 2010)	Captivity	6	50%	10%	5.0
5	Gates Creek	2007	Field	Adults tagged gastrically with acoustic transmitters and tracked through a fishway and to spawning grounds 55 km distance (Roscoe et al. 2011)	Turbulent and fast-flowing water, tagging	7	60%	29%	2.1
6	Late Shuswap	2002, 2003, 2006	Field	Adults captured by seine in the ocean 250 km from Fraser River mouth, tagged gastrically with radio transmitters, blood-sampled, tracked through Fraser River to spawning grounds (Martins et al. 2012b)	Temperature, tagging	8 9	14 °C: 14% 19 °C: 50%	14 °C: 5% 19 °C: 21%	14 °C: 2.8 19 °C: 2.4
7	Harrison River	2008	Lab	Adults held at 19 or 13 °C for 10 days, blood-sampled (Jeffries et al. 2012a)	Temperature, captivity	10 11	13 °C: 80% 19 °C: 100%	13 °C: 50% 19 °C: 53%	13 °C: 1.6 19 °C: 1.9
8	Summer runs	2010	Lab	Adults held in tanks at 21 or 16 °C and forced to burst swim for 3 min, exposed to air for 1 min, some fish then provided with AV, blood-sampled, observed for 15 days (Robinson et al. 2013)	Temperature, ES, air exposure, and AV	12 13 14	16 °C, no AV: 80% 16 °C + AV: 100% 21 °C: 100%	16 °C, no AV: 10% 16 °C + AV: 20% 21 °C: 100%	16 °C, no AV: 8.0 16 °C + AV: 5.0 21 °C: 1
9	Gates Creek	2007 and 2012	Field	Adults tagged gastrically with radio and acoustic transmitters near a dam and tracked through a fishway (Burnett et al. 2014a)	Turbulent and fast-flowing water to access fishway, tagging	15	62%	29%	2.1
10	Gates Creek	2013	Field	Adults tagged gastrically with acoustic transmitters near a dam and tracked through a fishway and to spawning grounds 55 km distance (Burnett et al. 2014b)	Turbulent and fast-flowing water to access fishway, tagging	16	56%	31%	1.8
11	Summer runs (Chilko, Horsefly, Mitchell)	2007	Lab	Adults held in tanks at 19 or 14 °C, all blood-sampled, observed for 7 days (Jeffries et al. 2014)	Temperature, captivity	17 18	14 °C: 30% 19 °C: 68%	14 °C: 20% 19 °C: 38%	14 °C: 1.5 19 °C: 1.8
12	Harrison River	2008	Lab	Adults held in tanks at 19 or 14 °C, all blood-sampled, observed for 5 days (Jeffries et al. 2014)	Temperature, captivity	19 20	14 °C: 60% 19 °C: 74%	14 °C: 19% 19 °C: 37%	14 °C: 3.2 19 °C: 2.0



Table A2 (continued).

Population (or Study run timing No. and group)		Study year	Lab or field	Study design and citation	Primary stressor(s)	Treatment No.	% mortality (female)	% mortality (male)	Relative magnitude of female mortality (female/male)
13	Weaver Creek	2008	Lab	Adults held in tanks at 19, 16, or 13 °C, forced to burst swim for 3 min, exposed to air for 1 min, all blood-sampled, observed for 2 days (Gale et al. 2014)	Temperature, ES, air exposure, captivity	21 22 23	13 °C: 12% 16 °C: 20% 19 °C: 40%	13 °C: 6% 16 °C: 10% 19 °C: 20%	13 °C: 2.0 16 °C: 2.0 19 °C: 2.0
14	Weaver Creek and Harrison River	2011	Field	Adults captured in Harrison River by seine, experimentally forced to burst swim for 3 min followed by 1 min air exposure, some given AV, all gastrically tagged with radio transmitters and tracked to spawning grounds ~3- to 6-week migration (Robinson et al. 2015)	ES, air exposure, some with AV, tagging	24 25 26	Control: 65% ES, no AV: 100% ES + AV: 100%	Control: 45% ES, no AV: 80% ES + AV: 90%	Control: 1.4 ES, no AV: 1.3 ES + AV: 1.1
15	Early Stuart	2013	Lab	Adults captured in lower Fraser River, brought to lab, manually entangled and released from a gill net after 20 s or 20 min, including 1 min air exposure, all fish biopsy-sampled except some controls, held under natural migratory thermal regime in tanks, observed till natural spawning date arrival ~3 weeks (Teffert et al. 2017)	GN entangled, air exposure, BS	27 28 29 30	Control: 15% Control + BS: 60% 20 s GN: 70% 20 min GN: 90%	Control: 7% Control + BS: 33% 20 s GN: 44% 20 min GN: 62%	Control: 2.1 Control + BS: 1.8 20 s GN: 1.6 20 min GN: 1.5
16	Late Shuswap	2014	Field	Adults captured in drift GN and BeS fisheries in lower Fraser River at sites 48 km (MacMillan Island, Mac) and 131 km (Peters Road, Pet) from ocean, all fish brought to shore, had radio transmitters gastrically inserted, were blood- and tissue-sampled, released and tracked to spawning grounds ~450 km from ocean and 2- to 3-week migration (Bass et al. 2018b)	Capture approach (GN or BeS), capture location (Mac or Pet), biopsy sampling	31 32 33 34	GN (Mac): 81% BeS (Mac): 30% GN (Pet): 60% BeS (Pet): 36%	GN (Mac): 50% BeS (Mac): 10% GN (Pet): 51% BeS (Pet): 30%	GN (Mac): 1.6 BeS (Mac): 3.0 GN (Pet): 1.2 BeS (Pet): 1.2
17	Summer runs (Chilko 50%, Nadina 30%, Stellako 10%)	2015	Field	Adults captured in drift GN and BeS fisheries in lower Fraser River at a site 131 km (Peters Road) from ocean, all fish brought to shore, radio transmitters gastrically inserted, were blood- and tissue-sampled, released and tracked to spawning river systems ~450 km from ocean and 2- to 3-week migration (Bass et al. 2018b)	Capture approach (GN or BeS), biopsy sampling, high migration temperatures (18–20 °C), tagging	35 36	GN: 100% BeS: 85%	GN: 100% BeS: 80%	GN: 1.0 BeS 1.1
18	Gates Creek	2016	Field	Adults captured at a fish weir near a dam on Seton River, tagged and tracked through a fishway and to spawning grounds 55 km distance, migrants experienced one of two flow regimes at the dam face and fishway entrance, spawning success was assessed in females by examining egg retention (Harrower et al. 2019)	Flow conditions (routine operations at flow conditions at dam: turbulent and fast-flowing water to access fishway; or alternative experimental flow conditions at dam: less turbulent water to access fishway), tagging	37 38	Routine: 55% Alternative: 25%	Routine: 25% Alternative: 18%	Routine: 2.2 Alternative: 1.4

**Table A2 (concluded).**

Study No.	Population (or run timing and group)	Study year	Lab or field	Study design and citation	Primary stressor(s)	Treatment No.	% mortality (female)	% mortality (male)	Relative magnitude of female mortality (female/male)
19	Gates Creek	2015	Field	Adults captured at a fish weir near a dam on Seton River, tagged with radio-tags, transported 6 km downriver into the mainstem Fraser River and tracked back to Seton River mouth, migrants experienced one of two whole riverine olfactory treatments after release, successful re-entering of Seton River was assessed (Drenner et al. 2018)	Stream olfactory conditions (routine dam operations or experimental diluted operations), tagging	39 40	Routine: 4% Diluted: 31%	Routine: 3% Diluted: 7%	Routine: 1.3 Diluted: 4.4
20	Chinook (Chilliwick)	2013	Lab	Adults captured at hatchery by dip net, brought to lab, manually entangled and released from a GN after 20 s, including 1 min air exposure, all fish biopsy-sampled except some controls, held under cool (9 °C) and warm (14 °C) conditions in tanks, observed for 4 days, which was time for fish in companion telemetry tracking study to migrate from release site back to hatchery (Teffer et al. 2018)	GN entangled, air exposure, captivity	41 42 43 44	Control 9 °C: 86% Control 14 °C: 100% GN 9 °C: 50% GN 14 °C: 71%	Control 9 °C: 37% Control 14 °C: 71% GN 9 °C: 46% GN 14 °C: 69%	Control 9 °C: 2.3 Control 14 °C: 1.4 GN 9 °C: 1.1 GN 14 °C: 1.0
21	Chinook (Chilliwick)	2013	Field	Adults captured at hatchery by dip net, transported downriver 40 km, all fish biopsy-sampled and implanted with radio transmitter, some fish manually entangled and released from a GN after 20 s, including 1 min air exposure, tracked to spawning grounds near hatchery ~4-day migration (Teffer et al. 2018)	GN entangled, air exposure, tagging	45 46	Control: 100% GN: 93%	Control: 24% GN: 61%	Control: 4.2 GN: 1.5
22	Coho (Chilliwick)	2012	Lab	Adults captured at hatchery by dip net prior to full sexual maturation, brought to lab, manually entangled and released from a GN after 20 s, including 1 min air exposure, all fish were blood- and tissue-sampled except some controls, held under cool (10 °C) and warm (15 °C) conditions in tanks, observed till natural spawning date in 2 weeks (Teffer et al. 2019)	GN entangled, air exposure, BS, captivity	47 48 49 50 51 52	Control 10 °C: 0 BS 10 °C: 5% GN + BS 10 °C: 10% Control 15 °C: 35% BS 15 °C: 40% GN + BS 15 °C: 75%	Control 10 °C: 0 BS 10 °C: 10% GN + BS 10 °C: 0% Control 15 °C: 0% BS 15 °C: 40% GN + BS 15 °C: 40%	Control 10 °C: 1.0 BS 10 °C: 0.5 GN + BS 10 °C: ∞ Control 15 °C: ∞ BS 15 °C: 1.0 GN + BS 15 °C: 1.9

**Note:** The percentages of female and male mortalities are provided separately along with the relative magnitude of female mortality calculated as the ratio of female to male mortality. Study No. corresponds to locations of studies on Fig. 1. There were 40 situations (Treatment No.) for studies dealing with sockeye salmon (Study Nos. 1–19, inclusive), where relative magnitude of male and female mortality could be calculated and compared, which are presented in Fig. 3. Population or run timing group indicates the sockeye group of study, except Study Nos. 20–22, which were other salmon species. In Study 22, two treatments resulted in some female mortality but no male mortality — with a zero denominator, the relative magnitude of female mortality could not be calculated and is indicated by ∞. Population natal areas are indicated on Fig. 1. Details on a study's design, primary stressors, and brief citation of the research are provided. Sample sizes for specific treatments can be found in the original papers. The order of the studies is largely based on publication date, with the full citation for each study in Table A1. AV = assisted ventilation; ES = exhaustive swimming; GN = gill net; BS = biopsy sampling; BeS = beach seine.