

Review

Release mortality in Pacific salmon fisheries along the homing migration and recommended best practices to maximize welfare and survival

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ARTICLE INFO

Keywords:

Delayed mortality
Size effects
Maturation
Mortality risks
Physiology
Female mortality bias
Best practices

ABSTRACT

Release or discard of captured fish commonly occurs in commercial and recreational fisheries and can result in immediate fish mortality during capture or delayed mortality upon release. This review synthesizes data from Pacific salmon (*Oncorhynchus* spp.) fisheries examining intrinsic and extrinsic factors affecting Pacific salmon individual release mortality (RM) across species and fishing sectors as adult fish mature and transit from marine, to estuarine, to fresh water. RM risk was high (26–45 % observed mortality) in all fisheries and environments when captured fish were bleeding, had high levels of scale loss, had fin or eye damage, and were exposed to low oxygen from net crowding and exhaustion. Highest RM risk (>45 % observed mortality) was associated with gill net and purse seine fisheries. Air exposure and handling duration contributed to high RM when water temperatures in any environment exceeded 18°C. Estuarine and lower river environments have elevated RM risk due to osmotic, maturation, and temperature changes. Short to medium term (≤24 h) observations were poor predictors of longer-term RM, and observations of at least 5–10 days were needed to assess more complete RM rates. RM mechanisms were environment, fishery sector, and life-stage specific. Our best practice recommendations for modifying current fishing practices are gear- and location-specific and aim to minimise stress, injury, and bycatch, which could result in improvements to fish welfare, reductions in RM, and associated conservation benefits.

1. Introduction

Release of captured fish occurs in commercial and recreational fisheries for a variety of reasons. Commercial marine fisheries discard ~11 % of global catches (Gilman et al., 2020), and recreational fisheries release at least 60 % of captured fish (Cooke and Cowx, 2004, 2006). Discarding bycatch (Alverson, 1994) or catch-and-release (a similar act in recreational fishing; Cooke and Cowx, 2004) is practiced as a way to meet harvest restrictions (e.g., size restrictions, fishing seasons, quotas) intended to improve the sustainability of fisheries, to meet market constraints or, for the case of recreational fisheries, to align with personal values (e.g., conservation ethic) (Arlinghaus et al., 2007; Catchpole et al., 2014). However, regardless of the intention, mortality of

released fish can be a substantial component of total fishing mortality which has contributed to the depletion of stocks and remains a critical problem in world fisheries (Coggins et al., 2007; FAO, 2012; Kelleher and Bank, 2015).

Upon interaction with fishing gear, fish exhibit an adaptive short-term ‘stress response’ involving behavioral reactions and secondary physiological changes (Wendelaar Bonga, 1997; Barton, 2002). Additionally, fish can be injured during the encounter, caused by hooks, nets, handling, or crowding (Chopin and Arimoto, 1995; Gilman et al., 2013). The duration and magnitude of fishing-related physiological stress and physical trauma can have fitness consequences in terms of immediate or delayed mortality across fishing sectors (Baker and Schindler, 2009; Cook et al., 2014; Wilson et al., 2014a). This phenomenon, recently

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<https://doi.org/10.1016/j.fishres.2025.107480>

Received 14 April 2025; Received in revised form 18 July 2025; Accepted 18 July 2025

Available online 2 August 2025

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termed “fishing-related incidental mortality” (FRIM; Patterson et al., 2017a), can occur regardless of whether fish are released intentionally or escape fishing gear before landing (Chopin and Arimoto, 1995; Baker and Schindler, 2009). From a management perspective, FRIM is problematic because unobserved mortality is difficult to estimate and thereby challenges the evaluation of fisheries sustainability (Patterson et al., 2017b; Hamel et al., 2023). From a conservation perspective, FRIM is wasteful, and international guidelines now call for bycatch mitigation as a means to attain the “United Nations Sustainable Development Goal 14: conserve and sustainably use the oceans, seas, and marine resources for sustainable development” (UNGA, 2015; Gilman et al., 2020). Minimizing FRIM and sublethal effects not only improves the sustainability of a fishery, but also protects the wellbeing and welfare of individual fish (Browman et al., 2019). However, doing so is complicated by the fact that fish response to fishing practices is context-specific, depending on region, gear type, species, population, life-history stage, and individual condition (Davis, 2002; Raby et al., 2015b). Understanding why fish die post-discard/release is a fundamental step towards minimizing FRIM.

It is believed that the single largest component of FRIM in most Pacific salmon (*Oncorhynchus* spp.) fisheries is associated with ‘release-mortality’ – fish that have encountered gear, were captured, and then intentionally released (Patterson et al., 2017b). Release mortality (RM) can occur in both Pacific salmon directed fisheries (i.e., size, species bycatch) and in non-directed fisheries. Although, some gear types, in particular set gill nets, are known for relatively high levels of escape mortality under particular circumstances (Baker and Schindler, 2009; Bass et al., 2018a), RM occurs in all sectors, gear types, and species.

Pacific salmon are an ideal group of species to study RM. Their anadromous life history requires annual migrations from oceans to natal freshwater spawning grounds (Groot and Margolis, 1991; Quinn, 2005). These directed and predictable movements towards known spawning locations facilitate harvest as large numbers of fish concentrate in migration pathways, during which they encounter fisheries that are diverse in social nature (commercial, recreational, Indigenous, subsistence, personal use), gear (e.g., seine net, gill net, rod and reel), and level of effort (e.g., number of boats, number of fishing lines, soak time, haul size). These fisheries occur at different stages of the migratory pathway, including offshore before beginning their spawning migration, and as they transition through the estuarine and freshwater portions of their migration, during which Pacific salmon cease feeding and undergo morphological and physiological transformations (Raby et al., 2015b). In addition to the gauntlet of fishing gear, migrating Pacific salmon contend with numerous challenges, such as changing ocean conditions (e.g., the “Pacific Blob”; Bond et al., 2015; Scannell et al., 2020), rapid shifts in temperature and salinity as fish transition from oceans to estuaries, high freshwater temperature or low discharge (features which are becoming more frequent due to climate change), and multiple anthropogenic habitat alterations in freshwater caused by various land-use practices (Muñoz et al., 2015; Grant et al., 2019; Crozier et al., 2021). This diversity in migratory environments and fishing factors complicates understanding RM, but also provides a unique opportunity to understand how Pacific salmon respond to the interactive effects of fisheries and their environment.

Pacific salmon have provided iconic cultural, nutritive, social, and economic value to Indigenous and non-Indigenous peoples (Jacob et al., 2010; Criddle and Shumizu, 2014; Atlas et al., 2021). Billions of dollars (U.S.) are spent annually on licenses, gear, fuel, and vessels resulting in the harvest of hundreds of thousands of tonnes of Pacific salmon by commercial, recreational, subsistence, personal use, and Indigenous sectors each year (Pacific Salmon Commission, 2016; Gislason et al., 2017; FAO, 2023; Alaska Department of Fish and Game 2024a,b,c). However, multiple species and stocks of Pacific salmon co-migrate, making it difficult for fisheries to avoid harvesting populations of conservation concern. Pacific salmon are also captured as bycatch in non-Pacific salmon directed fisheries, including in some of the world’s

largest fisheries (e.g., the Alaska pollock (*Gadus chalcogrammus*) fishery; Witherell et al., 2002; Stram and Ianelli, 2009; Lagasse et al., 2024). In response, increasingly more jurisdictions have implemented regulations to reduce Pacific salmon bycatch mortality in their policies and legislation, where Pacific salmon caught as bycatch are required to be released alive and with minimal injury (DFO, 2001; North Pacific Fishery Management Council, 2020). Given that many Pacific salmon populations are in decline (Grant et al., 2019), sustained bycatch means proportionally more fish within each population are being released post-capture than ever before, in accordance with selective fishing guidelines. Therefore, Pacific salmon not only serve as an ideal case study for examining RM, but a better understanding of the mechanisms and causes of RM can lead to improved capture and release approaches, thus helping with the conservation of these highly valuable species.

There have been several reviews which have summarized Pacific salmon behavioural and physiological responses to discarding and catch-and-release practices (Raby et al., 2015b; Patterson et al., 2017a; Cook et al., 2019b). However, there has been little research into, and no literature synthesis of, how RM or its causative factors change along the return-migration pathway as adult Pacific salmon pass through oceans, estuaries, and freshwater rivers. Earlier reviews focused only on specific fisheries (e.g., marine commercial fisheries; c.f. Patterson et al., 2017a; Cook et al., 2019b) or on general freshwater trends (Raby et al., 2015b). There is strong evidence that Pacific salmon resilience to capture and release increases with maturation or time spent in fresh water (Jeffries et al., 2012; Raby et al., 2013; Bass et al., 2018b), highlighting the context-specific nature of Pacific salmon responses to fishing location and life history stage. Thus, generalizations about RM, its causes, and potential solutions, are accompanied by substantial uncertainty if one extrapolates findings from different environments and fishery contexts.

The objective of this paper is to synthesize Pacific salmon behavioural, physiological, and survival responses to fishing gear interactions, including after fish are captured and released from gear, across all Pacific salmon fishing sectors, and to examine how responses change as fish mature, transition between different water environments, and migrate to spawning areas. Literature was identified using relevant search terms (e.g., “Pacific salmon”, “release mortality”, “beach seine”, “estuary”, “ocean”, “FRIM”) and focused on papers that examined and reported individual RM estimates for Pacific salmon. Where RM information for Pacific salmon was unavailable or limited for a particular fishery or location along the migration pathway, we extended our literature search to include studies on other salmonids. Although the scope of this review aims to consider all Pacific salmon fisheries and studies of individual RM, a large portion of the research on individual RM has been conducted on BC Pacific salmon, which have been conducted in collaboration with numerous Indigenous groups and stakeholders including fishers, government, and non-governmental organizations over the past 25 years. BC salmon fisheries are good model systems that reflect typical fisheries occurring in other jurisdictions and countries which have Pacific salmon. BC has five species of anadromous Pacific salmon (pink [*O. gorbuscha*], sockeye [*O. nerka*], coho [*O. kisutch*], chum [*O. keta*], and Chinook salmon [*O. tshawytscha*]) which comprise of hundreds of reproductively distinct populations (Holtby and Ciruna, 2007).

We begin with an overview of the methods used to examine the fish response to fisheries interactions and summarize the effects of fishing gears on Pacific salmon during capture, handling, and release. We then synthesize current knowledge on levels of RM associated with specific types of fisheries, and mechanisms underpinning RM based on fishing gear and capture, discard, and release practices (hereafter referred to as ‘capture and release’) in the three environmental phases of their spawning migration: marine, estuarine, and fresh water. Finally, we conclude by outlining science-based recommendations for fishery-specific best practices that fishers and managers could adopt or recommend to improve the welfare and survival of released fish, in an environment and fishery-specific context.

2. General overview of methods used to examine Pacific salmon response to fisheries release

Interaction with fishing gear and handling by fishers elicits an immediate stress response in fish that can be simplified into three phases: 1) release of catecholamine and corticosteroids by the hypothalamic-pituitary-interrenal axis and the autonomic nervous system, 2) tissue-level adjustments including elevated cardiac performance, redistribution of blood, osmoregulatory adjustments, and mobilization of energy stores, and 3) shifts in behaviour post-release or escape to regain homeostasis (Wendelaar Bonga, 1997; Barton, 2002). Depending on biotic (e.g., maturity, physical condition, size, sex) and abiotic (e.g., temperature, salinity, hydrology) factors and the severity of the fishery interaction, fish may survive the interaction, or develop sub-lethal effects – such as depressed reproductive hormones (Donaldson et al., 2014; Teffer et al., 2019), infections (Teffer et al., 2017, 2021), reduced metabolic scope (Clark et al., 2012; Raby et al., 2015a; Prystay et al., 2017), and reduced predator avoidance (Danylchuk et al., 2007; Raby et al., 2014a; Holder et al., 2020) – or experience immediate (i.e., at the time of capture, either still in the gear or onboard), short-term (i.e., released/discharged/escaped but dies within 24 h of the interaction; also referred to as acute mortality), or long-term (i.e., dies >24 h post-fisheries interaction; also referred to as delayed or latent mortality) mortality (Patterson et al., 2017a).

2.1. Physiological and physical assessment metrics

Physiological analyses are invaluable for identifying the mechanistic causes of RM when coupled with behavioural or survival measures (e.g., Donaldson et al., 2008, 2011; Cooke et al., 2013; Raby et al., 2015c; Teffer et al., 2018; Bass et al., 2018a). Blood-based biomarkers (e.g., glucose, lactate, cortisol, inorganic ions) – typically collected from the caudal vasculature (Lawrence et al., 2020) – and metabolic rate (e.g., metabolic oxygen consumption, heart rate) are some of the most common physiological metrics used for assessing fish condition, the magnitude of physiological response (disturbance from homeostasis), and recovery duration. Monitoring metabolic rate can provide real-time physiological response and recovery (Donaldson et al., 2010; Eliason et al., 2013b; Raby et al., 2015a; Prystay et al., 2017); however, technological limitations challenge its application in the field. Blood parameters are useful because anaerobic metabolism is indicative of burst swimming and hypoxia, both common responses to fisheries interactions. As tissue oxygen supplies become depleted, metabolic processes transition to being fueled by anaerobic breakdown of glycogen into glucose by white muscle fibers, producing lactic acid as a by-product (Wood, 1991; Milligan, 1996). This process is referred to as anaerobiosis and can lead to potential behavioural impairment and cardiac arrest. If prolonged, anaerobiosis may also lead to acidosis, where lactate among other metabolic protons (e.g., K^+ [hyperkalaemic]) accumulate in both the muscle and blood causing osmoregulatory imbalance. Elevated CO_2 partial pressure also increases the concentration of HCO_3^- and H^+ in the blood, which ultimately decreases pH (i.e., venous blood becomes acidic and hypoxemic). Hence, measuring lactate concentrations in the blood can indicate anaerobiosis and potential plasma acidosis, meanwhile increases in glucose can indicate energy mobilization stimulated by stress hormones (Kieffer, 2000; Barton et al., 2002). Plasma cortisol is the primary stress hormone, where higher cortisol levels increase energy mobilization but can also act as an immunosuppressant (Schreck et al., 2001). Finally, plasma osmolality, sodium, and chloride concentrations serve as indicators of osmoregulatory status (Barton et al., 2002).

In addition to blood sampling, non-lethal tissue biopsies, such as gill filament tips, scales, skin, fin, or muscle (e.g., Beacham et al., 2004; Donaldson et al., 2011; Teffer et al., 2021; Lunzmann-Cooke et al., 2024) have recently been used in genetic stock identification (Beacham et al., 2004, 2021b, 2022) and sex determination (Beacham et al., 2017;

Lunzmann-Cooke et al., 2024). This type of biological sampling has also been used to examine gene expression, which has provided ground-breaking insights into immune response, diseases, and cellular stress (e.g., Bass et al., 2019; DePasquale et al., 2023; Donaldson et al., 2014; Jeffries et al., 2021; Miller et al., 2017; Teffer et al., 2017, 2018) associated with fisheries interactions and the physiological mechanisms underpinning RM.

Visible physical injury assessments are commonly conducted in studies of RM because injuries to the body, eyes, and scales can compromise osmoregulatory function (Teffer et al., 2017; Cook et al., 2019a), impair swimming (Nguyen et al., 2014; Lunzmann-Cooke et al., 2024), and facilitate infections (Teffer et al., 2017, 2018; Bass et al., 2019; Hinch et al., 2024), yielding latent effects on survival (Raby et al., 2015b; Teffer et al., 2017; Bass et al., 2018a; Cook et al., 2019a; Hinch et al., 2024; Lunzmann-Cooke et al., 2024). Injury is typically assessed according to scale loss, net or line scars – which are identified as dark contusion lines on the head and body, damaged fins (e.g., fraying and tearing – fin ray separation) – hooking related tissue and eye damage, or other dermal wounds. Scale loss can directly impact osmoregulation (Cook et al., 2019a; Olsen et al., 2012; Zydlewski et al., 2010) and when combined with excess mucus loss can be particularly impactful because they provide a primary barrier to infections (Baker and Schindler, 2009; Teffer et al., 2017). The negative relationship between scale loss and survival is not unique to Pacific salmon, as scale loss has also been attributed to reduced survival in other fish species (e.g., Atlantic herring [*Clupea harengus*]; Olsen et al., 2012; Veldhuizen et al., 2018). Research has generally focused on examining the effects of injuries independently, however, it is suspected that cumulative impact of multiple injuries can strongly influence RM risk.

Vitality scores (e.g., RAMP - reflex action mortality predictors) are rapid methods for assessing behavioural impairments usually associated with exhaustion and fatigue (Davis, 2010; Raby et al., 2012a, 2013, 2015c; McArley and Herbert, 2014; Cook et al., 2019a; Lennox et al., 2024). RAMP scores are determined by quantifying reflexes, where the five most commonly used ones for the study of fisheries interactions are tail grab, body flex, head complex, orientation, and vestibular-ocular response (Lennox et al., 2024). These reflex responses require the use of white muscles (e.g., burst swimming in response to tail grab), where lack of a response may indicate metabolic acidosis and exhaustion, or a drop in oxygen partial pressure in the blood causing the fish to lose consciousness (e.g., loss of orientation) (Raby et al., 2012a, 2013, 2015c). Hence, vitality scores are a validated, cost-effective, real-time proxy for assessing physiological departure from homeostasis (i.e., impairment), useful to those studying RM (Davis, 2010; Raby et al., 2012a; Brownscombe et al., 2013; Raby et al., 2015c; Lennox et al., 2024).

2.2. Study approaches: holding experiments vs. telemetry

Experimental simulations in laboratories (e.g., using nets, exhaustive exercise, and/or air exposure; Gale et al., 2011; Prystay et al., 2017; Teffer et al., 2017) and experiments in the field either with actual fishery methods or in conjunction with actual fisheries (e.g., Raby et al., 2014a; Cook et al., 2019a; Johnston et al., 2021; Elmer et al., 2022; Hinch et al., 2024; Lunzmann-Cooke et al., 2024) have been used to examine the individual and joint effects of fisheries catch and release interactions, such as exhaustive exercise, air exposure, and net entanglement. Holding studies of varying durations involving fish placed into tanks in the laboratory or net pens in the wild following fisheries interactions allows individuals to be repeat sampled pre-capture (lab studies) and post-capture (lab and field studies) (Gale et al., 2011; Donaldson et al., 2011a; Robinson et al., 2013; Donaldson et al., 2014; Gale et al., 2014; Raby et al., 2015a, d; Robinson et al., 2015; Raby et al., 2015c; Prystay et al., 2017; Teffer et al., 2017; Cook et al., 2018b; Teffer et al., 2018; Bass et al., 2019; Cook et al., 2019a, a; Teffer et al., 2019; Kraskura et al., 2020; Eliason et al., 2020; Teffer et al., 2021). The advantage of holding

studies is that fate of fish can be accurately determined, components underpinning mortality can be isolated (e.g., net, lure, crowding effects), and repeat sampling provides insight into the physiological mechanisms of capture, potential recovery, and mortality. However, the lack of realism and management applicability of holding studies must be acknowledged. In confinement, fish are protected from deleterious environmental conditions (e.g. predators, poor water quality) that might be present where the fishery takes place, thus mortality rates might be an underestimate of those in the wild. On the other hand, holding studies can introduce confounding stressors via effects of captivity (e.g. spread of disease, exacerbate fish stress; (Patterson et al., 2004; Raby et al., 2015c) and transportation if fish need to be moved significant distances to holding locales (e.g. Gale et al., 2011; Teffer et al., 2017), which might result in an overestimate of mortality rates compared to those in the wild.

Short monitoring periods were common in early holding studies (e.g., 1–5 days) which produced very low rates of mortality associated with capture and release (e.g., Gjernes et al., 1993; Washington Department of Fisheries et al., 1993; Brobbel et al., 1996; Candy and Carter, 1996; Cox-Rogers et al., 1999; Diewert et al., 2002; Buchanan et al., 2002). More recently it's been found that 5–10 days are often needed in holding studies for survival consequences to become apparent (Gale et al., 2011; Donaldson et al., 2011a; Raby et al., 2015b; Teffer et al., 2017; Hinch et al., 2024). For instance, a holding study that exposed sockeye salmon to a simulated catch-and-release event before monitoring recovery in tanks at 21°C reported survival to have declined from 100 % at 48 h post-fisheries simulation to 19 % after 72 h (Gale et al., 2011). Given the issues discussed above, care must be taken in interpreting the results of holding studies if using to develop estimates of RM.

Telemetry studies are the other main approach to examine RM in Pacific salmon. Tagged fish can be monitored beyond the location of the fishery interaction in their natural habitat where they are exposed to predators and other typical environmental features (Donaldson et al., 2008; Cooke et al., 2008; Raby et al., 2014b; Elmer et al., 2022), and they are permitted to continue on their migrations (Hinch et al., 2006; Wilson et al., 2014b). Further, releasing fish after capture eliminates captivity and transportation effects of holding studies, and Pacific salmon equipped with acoustic transmitters typically have better survival rates (i.e., lower time-specific mortality) than individuals monitored in captivity (Donaldson et al., 2011a; Raby et al., 2015c). However, telemetry studies have limitations (e.g., Dick et al., 2020). Once released, no further physiological information can be collected from tagged fish unless they are recaptured and resampled. The accuracy of mortality and travel speed estimates is limited by the tag type and the number, locations, and detection efficiency of receivers in the study system. This also means that if fish do not swim along the anticipated migration route, non-detection may be counted as a mortality, despite the fish being alive. When Pacific salmon are captured in marine environments, uncertainty related to genetic stock assignment (Beacham et al., 2021a), natural or fishery influenced straying (Candy and Beacham, 2000; Ford et al., 2015; Bett et al., 2017), or predation (Raby et al., 2014b; Chasco et al., 2017) may decrease the accuracy of RM estimates. Further, tag losses, natural mortality, or unreported harvest of tagged individuals can bias estimates of survival because researchers may ascribe these events as a mortality event related to the fishery encounter (Cooke et al., 2006). As such, RM estimates derived from telemetry are often assumed to be maximum values. The strongest study design is to combine telemetry field studies with lab-holding experiments, which can generate both a mechanistic understanding and RM estimates from two divergent approaches. Hinch et al. (2024) adopted this dual approach in their study of RM in marine recreational Pacific salmon fisheries finding nearly identical RM estimates from both study approaches, which enabled the researchers to confidently propose strong science based best practices for capture and release.

2.3. Handling and bio-sampling effects

All physiological, physical, or vitality assessments conducted on captured Pacific salmon require different types of handling by investigators. Some types of investigator handling may mimic aspects of capture and release by exposing fish to air, manipulating them out of gear, gripping the caudal peduncle while tagging, etc. However, some aspects of handling (e.g., biopsy or blood sampling) are unique to these studies and they could have adverse effects on fish physiology and survival by causing additional stress and injury, which may affect estimates of mortality (Cooke et al., 2005, 2011; Raby et al., 2012a; Teffer et al., 2017; Wilson et al., 2017; Dick et al., 2018; Teffer et al., 2018, 2019). For instance, a holding study examining the effects of angling catch and release on Chinook salmon observed that infectious outbreaks first appeared on parts of the body where fish were held during sampling (K.M. Zinn pers. obs). Recently, studies have begun to incorporate a 'biopsy control group' in study designs (Teffer et al., 2017, 2018, 2019, 2021; Bass et al., 2019) in an attempt to parse out variability in survival and physiology attributable to taking a biopsy.

It is possible that even the simple act of tagging could affect survival of capture and released fish (Runde et al., 2020, 2022), yet tagging effects are difficult to assess due to lack of true controls. The location of tag attachment varies among studies, often due to migration stage. Esophageal insertion is generally used when Pacific salmon are no longer feeding (e.g. as they embark on upriver migrations) (Cooke et al., 2012; Corbett et al., 2012), whereas external attachment is required if fish are still feeding (Raby et al., 2015c). Neither method requires anesthesia, enabling Pacific salmon to recover quickly and reduces handling time. Dick et al. (2018) found that the capture and handling process of both methods yielded similar acute physiological disturbances – there was limited evidence of additive effects from the tags themselves. Gastric tagging reduces handling time to one third of that required for external tagging (average 15 sec vs 43 sec), minimizing potential effects of handling. However, gastric tagging also risks perforating the stomach, which could have physiological consequences and remains poorly understood (Corbett et al., 2012; Dick et al., 2018, 2020). That said, stomach perforation during gastric tagging is rare (Dick et al., 2018); therefore, it remains a preferred tagging method due to the short handling time and lack of anesthetic.

3. Primary effects of fishing gear

Pacific salmon are predominantly captured using either net-based fisheries – specifically gill net, trawls (although incidental and Pacific salmon are not retained; North Pacific Fishery Management Council, 2023), purse seines, and beach seines – or hook and line-based fisheries, mainly trolling and angling (DFO, 2023a,b). Other gear types are also used to target Pacific salmon – particularly with Indigenous fisheries (e.g., fish wheels, dip nets, and weirs) – however, these approaches have not been extensively studied with respect to RM. Consequently, research examining RM in salmonids has predominantly focused on net-based and hook and line-based fisheries.

3.1. Net-based fisheries

3.1.1. Gill nets

Gill net fisheries, including drift, set, and tangle nets, capture fish by ensnaring them in the mesh. Gill nets are used by both commercial and Indigenous fisheries as their simplicity and relatively lower costs to deploy enables them to be used in marine, estuarine, and freshwater systems (Patterson et al., 2017a). Gill nets (both drift and set nets) have a mesh designed to capture fish by their gill, between the opercula and the dorsal fin. By ensnaring around the body and gills, gill nets cause asphyxiation, scale loss, dermal injury, and stimulate burst swimming, which can ultimately lead to anaerobiosis and acidosis (Kojima et al., 2004; Bass et al., 2018a). In some cases, net abrasion during

entanglement may cause bleeding from the gills (Raby et al., 2013). Tangle nets have a smaller mesh size intended to capture fish by tangling around their nose, jaws, teeth, or fins instead of their body, mitigating some of the risks associated with gill nets. However, there are still instances where tangle nets encircle the operculum. Tangle nets generally have greater post-release survival compared to other types of gill nets, but are typically only used by researchers or management agencies (Raby et al., 2015b; Reid, 2020; Elmer et al., 2022). Both gill and tangle nets have a soak time ranging from several minutes to hours including overnight sets, exposing fish to prolonged tissue anoxia, blood lactic acid acidosis, and depredation (Uhlmann and Broadhurst, 2015; Patterson et al., 2017a). Once fish are pulled onboard for detangling and processing, they are further subjected to air exposure and injury from handling prior to being discarded. Despite being simple to use, it is not uncommon for fish to escape gill nets (Baker et al., 2011; Bass et al., 2018a). In this case, individuals are not subjected to handling stress, but they may still get injured.

3.1.2. Purse seines

Unlike gill nets, purse seines are primarily confined to marine environments and consist of a vertical net deployed from a fishing vessel that captures fish by encircling schools of fish and drawing the bottom closed. Hence, most species within the vicinity of a purse seine may be captured, and fish are crowded into a confined area. A purse seine tow can last several minutes (Raby et al., 2015c; Cook et al., 2018a, b; Reid, 2020), where fish may undergo exhaustive exercise as escape attempts increase. Stress is exacerbated by water volume and oxygen levels progressively declining as the net constricts while being pulled closer to the vessel and when fish are confined in a brailer for transfer onboard. Furthermore, fish may experience fin damage, bruising, and crushing injuries as they run into one another and into the net itself (Raby et al., 2015c; Cook et al., 2018a, b; Reid, 2020). Once landed, fish are then sorted on deck prior to being released. Sorting further exposes fish to bouts of exhaustive exercise, air exposure, and injury including scale loss from rubbing against the boat surfaces, other gear, and physical handling (Cook et al., 2018b, 2019a).

3.1.3. Trawls

Trawls are used by commercial marine fisheries in which Pacific salmon are frequently caught as bycatch and are often released (North Pacific Fishery Management Council, 2023; Lagasse et al., 2024). Trawl fisheries involve towing a large net behind a boat and capturing fish by confining them in the cod end (back of the net). As with purse seines, captured fish undergo exhaustive exercise as they burst swim trying to escape the net and exhibit physical damage from one another, the net itself, or the side of the boat, due to crowding, crushing, and confinement (Chopin and Arimoto, 1995; Ryer, 2004; Cook et al., 2019b). Once landed, fish are sorted during which they may be air exposed for more than 60 min (Parker et al., 1959; Uhlmann et al., 2016). Sorting may further injure fish, including scale loss and bruising from interactions with the boat, other gear, and handling.

3.1.4. Beach seines

Beach seine fisheries are conducted in estuarine and riverine systems. These fisheries involve using a net with floats on the topside and weights on the bottom to encircle fish and pull them to shore. This is typically done with one end of the net anchored on shore and the other deployed by a boat with the current. The unanchored end is then brought onshore, and both ends of the net are pulled shoreward and together. If water levels are high or the velocity is fast, fish sorting is more difficult and handling time increases. Crowding fish by pulling the net closer to shore where it is shallower facilitates sorting but increases the risk of injury to fish as they are more likely to bump into or rub against one another, the substrate or the net. Additionally, crowding in a beach seine diminishes the water quality in the net because shallow water is often warmer, and fish consume local oxygen more rapidly

(Raby et al., 2014a).

3.2. Hook and line fisheries

3.2.1. Commercial Trolling

Trolling is used in commercial, Indigenous, and recreational fisheries in marine and estuarine environments. Trolling fisheries involves multiple lines each with multiple hooks and lures or bait at different depths pulled behind a boat – specific type or arrangement of this gear varies according to target species and the specific fishery. Commercial troll fisheries are often associated with larger gear and hooks, faster trolling speeds, less active line monitoring, and deploying several hooks along the same line capturing multiple fish at a time. Together, these factors can significantly increase the time on a hook relative to recreational trolling fisheries. Injuries and stress during capture and landing in commercial troll fisheries are similar to that of recreational angling (including trolling; described below), although given numerous fish may be captured at one time with commercial trolling equipment, the risk of physiological exhaustion and depredation is greater. Few studies have estimated RM associated with commercial trolling fisheries where release mortality estimates range between 8 % and 20 % – all of which have involved holding studies or estimated mortality according to assumptions associated with injury severity (Parker and Black, 1959 [coho salmon]; Parker et al., 1959 [chinook salmon]; Davis et al., 1985 [chinook salmon]; Wertheimer, 1988 [coho salmon]; Orsi et al., 1993 [chinook salmon]). RM may be enhanced when trolling speeds are fast because speed is more likely to increase the likelihood of exhaustion while being dragged by unattended gear, and with the use of relatively large hooks which are more likely to cause injury than smaller hooks particularly if hooking injury occur to the eye and gills (Hinch et al., 2006; Orsi et al., 1993; Wendelaar Bonga, 1997). Nevertheless, Pacific salmon captured by trolling are typically hooked in the outer mouth and jaw (Cox-Rogers et al., 1999), both hooking locations known to cause less RM than when hooked deeper in the mouth (Wertheimer, 1988), which is more common in hook-and-line fisheries that use natural baits and passive angling techniques (Muoneke and Childress, 1994).

3.2.2. Recreational Angling

Recreational angling (e.g., trolling, down rigging, jigging, bottom bouncing) occurs throughout the marine, estuarine, and non-spawning lake and riverine regions associated with Pacific salmon migrations. A recent survey of > 1500 marine anglers in BC indicates recreational anglers target Pacific salmon using various hook sizes, lures, and natural and artificial baits (Hinch et al., 2024), and flies (common in the riverine system). As with commercial trolling, angling can cause lethal bleeding and puncture wounds, particularly if fish are hooked in gills, eyes, or internally (e.g., esophagus) rather than the maxillary, upper jaw, or mouth cavity (Courter et al., 2023; Lindsay et al., 2004). Risk of severe injury increases when hook size is large compared to fish fork length and the relative mouth size (Hinch et al., 2024). Similarly, hooks with large gaps between the point and the shank cause deeper wounds which are more lethal as there is greater risk of damaging blood vessels and nerves linked to the cardiovascular systems and gills (Gjernes et al., 1993), and ocular nerves, blood vessels, and eyes (Hinch et al., 2024). However, hooks that are small relative to the size of the fish increases the probability of the hook being ingested when passively fished (Alós et al., 2008). In freshwater angling, fly fishing gear is typically associated with less injury as fish rarely swallow the hook and the hook is therefore easier to remove – both features lowering the risk of RM (Arlinghaus et al., 2007; High and Meyer, 2014). RM was five to eight-fold lower in fly-caught rainbow trout (*O. mykiss*) compared to individuals caught using bait (Schisler and Bergersen, 1996). Similarly, barbless hooks are more easily removed than barbed hooks, and their use can reduce handling time and injury (Cooke et al., 2001; Thorstad, 2003; Patterson et al., 2017a) although it is unclear if barbless hooks reduce mortality (e.g., Schill and Scarpella, 1997). Regardless of hook or bait type, once

hooked, fish experience elevated stress and exhaustion as they attempt to escape. Risk of RM is further enhanced with longer angling and handling times (i.e., time from hooking to release) which can be caused by increases in fish size and decreases in angler experience (Thorstad, 2003; Arlinghaus et al., 2007).

Once captured, fish are usually exposed to air while dehooking and measuring, or for photography (Arlinghaus et al., 2007; Pelletier et al., 2007). Small dip nets are often used to facilitate complete capture and then release from the hook with the belief that it reduces handling time and injury. However, they generally extend the holding time, or in some cases cause additional physical injury to fish (Hinch et al., 2006; Lizée et al., 2018). The same BC angler survey revealed that 8.8 % of fish were air exposed for two-minutes or greater with an average of 40 s (Hinch et al., 2024), thus most angled fish are exposed to only modest levels of air yet some are clearly exposed to levels that research suggests causes delayed mortality (Cook et al., 2015).

4. Fishing interactions along the migration pathway

Mechanisms underpinning RM depend heavily on the environmental context, fish physiological and physical status, and type of gear and handling practices used (Davis, 2002; Raby et al., 2015b; Fig. 1). Pacific salmon experience saline and generally cool water while migrating through coastal marine environments. As they enter estuarine areas, salinity declines and, during the summer and early fall, temperatures start to increase. Once in rivers, temperatures increase further in the summer and early fall, and can reach sub-optimal or even lethal levels

(Eliason et al., 2011; Martins et al., 2011; Hinch et al., 2024). Hence, the context of RM evolves as Pacific salmon progress along their migratory pathway from the marine environment to terminal spawning grounds upriver (Fig. 1). The subsequent sections contextualize the dominant mechanisms by which each fishing gear type affect RM along the three environmental phases of the Pacific salmon homing migration (marine, estuarine/lower river, and upper fresh water/terminal tributary), including short-term and long-term effects.

Few studies have directly compared RM levels among gear, and when comparisons were made, they involved only a couple types (e.g., Donaldson et al., 2011, 2012; Robinson et al., 2013; Raby et al., 2013; Bass et al., 2018b; Teffer et al., 2021; Elmer et al., 2022). Although several studies provide RM (Table 1), it is important to note that in addition to the biological and environmental contexts, RM also depends on cumulative effects of capture (e.g., gear and soak time) and handling (e.g., air exposure, gear selection) and studying RM also depends on those factors as well as the study design (e.g., monitoring duration, sample size). In many cases, treatments within and among studies differ by more than one effect (e.g., air exposure, handling time, net mesh size) such that RM cannot simply be calculated by taking the average mortality across treatments. Population-specific differences further complicate RM among gears, occasionally yielding conflicting trends (Donaldson et al., 2012). Therefore, we aligned fisheries treatments to the likelihood of mortality occurring (“low risk” to “very high risk”; Table 1), enabling fishing practices underpinning high RM to be discerned. In this case, RM risk score was assessed relative to RM levels determined from control or baseline states identified in a study, where

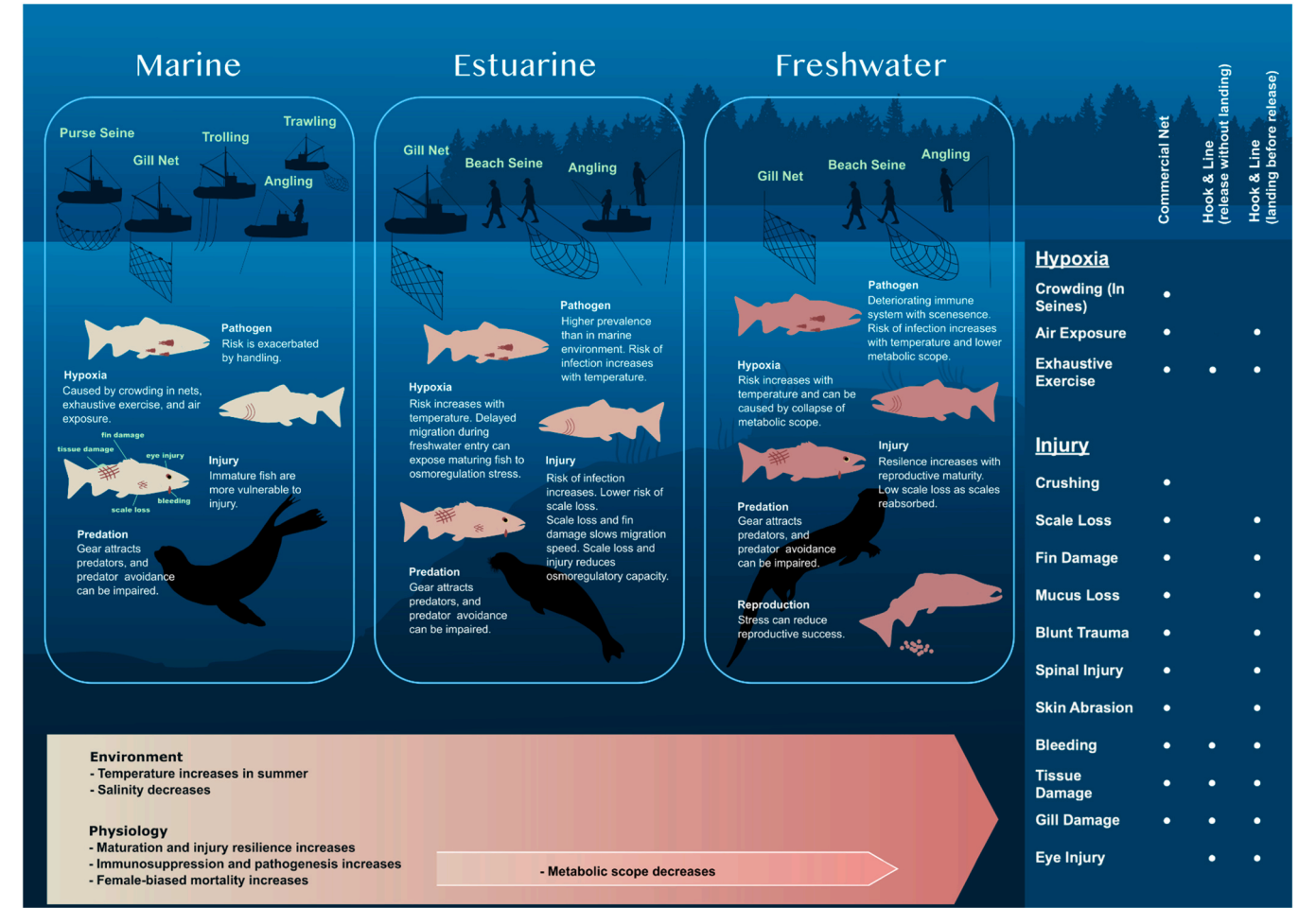


Fig. 1. Schematic diagram outlining mechanisms underpinning release mortality (RM) in Pacific salmon fisheries along the homing migration. [Artwork by Sofia Jain-Schlaepfer].

Table 1

Summary from studies estimating RM in British Columbia Pacific salmon fisheries in relation to migration stage, gear type, species and specific fishery variables that can lead to RM. Study design refers to whether telemetry and/or holding experiments were employed. Immediate RM is the proportion of fish that died sometime between capture and release; short-term RM is the percentage that died within 24 h post-release; and delayed (long-term) mortality is the percentage that died after 24 h post-release (duration and/or distance in kilometres (km) or river kilometers (rkm) is specified). RM estimates represent the direct estimates from studies and control RM estimates are shown when they were estimated. RM risk is a qualitative assessment based on professional judgment of the expected level of RM according to gear, handling methods, observed impairment, maturation stage, risk of infection, and environmental conditions examined in each study. RM risk score is assessed relative to RM levels determined from control or baseline states. Only one risk score was created for studies that did not include more than one fishery treatment. Low risk corresponds to 0–5 % observed RM; Moderate risk corresponds to 6–25 % observed RM; High risk corresponds to 26–45 % observed RM; Very high risk corresponds to > 45 % observed RM. Risk of female-biased mortality is indicated as ‘present’ if the study reported either higher female mortality rates or higher injury or RAMP scores where sex-specific mortality was not calculated.

Migration stage	Gear	Pacific salmon species	Fishery variables tested	Study design	Empirical RM estimates			RM risk			Source
					Immediate	Short-term	Long-term	Severe interaction	Minor interaction	Female bias	
Marine	Purse seine	Chum	Time pursued Air exposure Crowding	Holding ¹ (N= 360)	Air exposure >5 min: 5%	NA	Up to 5 days All treatments: 11% Control: 0% Up to 10 days Total: 3.6% Control: 0%	Very high risk ³ - Crowding ⁴ - Pursued >15 min - Air exposure ≥6 min	Low risk ³ - No crowding ⁴ - Pursued < 15min - Air exposure <3 min	Present	Cook et al. 2018b
		Coho	NA	Telemetry ² (N=43) & Holding ² (N=118) - 20min tow - 24min pursued - no crowding - 20sec air exposure	Telemetry + holding 2%	Holding 24 hr: 21%	Telemetry ~95 hr: 20% 10-20 days: 47%	Very high risk	NA	NA	Raby et al. 2015c
		Coho	NA	Telemetry ¹ (N=220) - 33min tow - 13min air exposure	4%	4.6 days: 36%	Release to: 43-56 km: 34% 78 rkm upstream: 72%	Very high risk - Impaired body flex ⁵ - ≥25% scale loss	Moderate risk - Unimpaired body flex ⁵ - No scale loss	NA	Cook et al. 2018a
	Sockeye	Soak time	NA	Telemetry ³ (N = 183)	NA	NA	Up to 60 days (200 rkm) Treatments pooled Total: 25% Pre-river entry: 4% Post-river entry: 21% By time pursued <15 mins: 22% 30-45 min: 29%	High risk - Pursued 30-45min	Moderate risk - Pursued <15min	Present	Reid 2020
				Ocean vs river-capture Temperature	NA	NA	~400 km Capture location: Ocean: ~20% River: ~60%	Very high risk - River-captured - >18°C water temperature	Moderate risk - Ocean-captured - <19°C water temperature	NA	Martins et al. 2011
	Angling	Coho	Air exposure Hook size - Barbless, 3/0-6/0 siwash and octopus hooks - Knotless, vinyl-coated landing net	Telemetry ² (N = 403)	1.5%	NA	Median 3.3 days (50 km): 32% Median 9 days: 56% ⁶ Median 13.4 days: 77% ⁵	Very high risk - Scale loss >35% - Eye injury - Major bleeding - Small fork length	Low risk - Scale loss <5% - No eye injury - No bleeding - Large fork length	Absent	Lunzmann-Cooke et al. 2024
		Chinook	Air exposure Gear type Handling and landing	Telemetry ² (N = 464)	1.2%	NA	10 days to 23 weeks (~80–100km) Total ⁷ : 16% By fork length: >80 cm: 9% 62–79 cm: 19% <62 cm: 20% By injury and handling severity: Good condition: 3% Moderate injury (not involving eyes): 15% Severe injury (not involving eyes): 23% Eye injury: 22%	High risk - Large hooks (7/0 Siwash “commercial” hook, 38mm gap width) - Landing fish on deck - Use of a landing net of any kind - Fork length < 62 cm - Major bleeding - Eye injury - Scale loss	Low risk - Small hooks (3/0 Octopus with gap width = 15mm) - De-hooking under water - Fork length > 80 cm - No eye injury - No bleeding	Absent	Hinch et al. 2024
	Chinook	Gear type Hook type In-line flasher Gaff release	NA	Holding ^{1,2} (N = 490)	8%	1%	Up to 10 days By fork length: <45 cm: 30% 45-61 cm: 34% 62-80 cm: 11% ≥80 cm: 9% By injury and handling severity: Good condition: 4% Moderate injury: 23% Severe injury: 30% Eye injury: 26% By hook type: Single hook: 28% Treble hook: 37% By bait type: Artificial bait: 35% Live bait: 28% By hook and bait type: Single hook + artificial bait: 29% Single hook + live bait: 27% Treble hook + artificial bait: 45% Treble hook + live bait: 29%	Very high risk: - <45 cm fork length - Treble hooks - Artificial bait - Severe scale loss - Severe fin damage - Severe bleed	Low risk - ≥62 cm fork length - Single hooks - Minor fin damage - Minor scale loss - Minor bleed - No eye damage	Present	Zinn et al. 2024*

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Table 1 (continued)

Marine to Estuarine	Angling	Chinook	Air exposure Handling gear	Telemetry ² (N = 322)	1%	NA	5 days Total: 12% By fork length: >70 cm: 12% <70 cm: 19% Air exposure 5min: 50%	Very high risk - 5 min air exposure	Moderate risk - No air exposure	Present	Hinch et al. 2024
Estuarine to Early freshwater	Beach Seine	Coho	Assisted recovery	Telemetry ² (N=182) - Median entanglement 3min 20s	3%	NA	48h: 19% Release to spawning habitat (>300km) ⁸ : 39% Control ⁶ : 23%	Moderate risk	NA	NA	Raby et al. 2014a
	Gill net	Sockeye	Air exposure	Holding ² (N = 52)	NA	NA	Up to 40 days ⁷ Control: 11% Control + Biopsy: 47% Gill net (20 sec): 57% Gill net (20 min + 1 min air exposure): 76%	Very high risk - 20 min entanglement - 1 min air exposure	Moderate risk - 20sec entanglement	Present	Teffer et al. 2017
		Sockeye	Air exposure Injury Assisted recovery	Telemetry ² (N = 238)	NA	NA	Gill net injury 38 rkm (24-48h): 10% 145 rkm (7 days): 40% 400 rkm: 64% No gill net injury 38 rkm (24-48h): 11% 145 rkm (7 days): 34% 400 rkm: 50% Air exposure 38 rkm (24-48h): 7% 145 rkm (7 days): 38% 400 rkm: 59% No air exposure 38 rkm (24-48h): 14% 145 rkm (7 days): 36% 400 rkm: 55% Assisted recovery 38 rkm (24-48h): 11% 145 rkm (7 days): 38% 400 rkm: 61% No assisted recovery 38 rkm (24-48h): 10% 145 rkm (7 days): 35% 400 rkm: 53%	Very high risk - Injury caused by 30s gill net - 2min air exposure	Moderate risk - Injury - No air exposure	NA	Nguyen et al. 2014
		Sockeye	Temperature Captivity Location (river vs marine)	Holding ² (N = 185)	NA	NA	Up to 4 weeks Marine, 14°C Gill net + air exposure: 6% Control + biopsy: 0% Control: 0% Marine, 18°C Gill net + air exposure: 100% Control + biopsy: 100% Control: 19% River, 14°C Gill net: 32% Gill net + biopsy: 55% Beach Seine: 0% Beach seine + biopsy: 14% River, 18°C Gill net: 50% Gill net + biopsy: 100% Beach Seine: 89% Beach seine + biopsy: 100%	Very high risk - >18°C water - >20s gill net - 1 min air exposure - Marine or river-collected	Moderate risk - 14°C water - 20s gill net - 1 min air - Marine collected	Present	Teffer et al. 2021
Freshwater	Gill net	Chinook	Temperature Air exposure	Telemetry ² (N = 58) & Holding (4 days) - 20s gill net - 1min air exposure (holding study only)	Holding (both temps.) ~30%	NA	14 days – Telemetry Biopsy: 52% Gill net: 69% 4 days – Holding 9°C Control: 50% Gill net: 47% 14°C Control: 76% Gill net: 70%	Very high risk - 14°C water ⁹	Moderate risk - 9°C water	Present	Teffer et al. 2018
		Coho	Temperature Air exposure	Holding ² (14 days; N = 240)	NA	NA	14 days 10°C Control: 2.5% Gill net + biopsy: 3% Biopsy: 13% 15°C Control: 22% Gill net + biopsy: 65% Biopsy: 41%	Very high risk - 15°C water ⁹ - 20s gill net - 1 min air exposure	Moderate risk - 10°C water - 20s gill net - 1min air exposure	Present	Teffer et al. 2019

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Table 1 (continued)

	Chinook	Air exposure	Telemetry ² (N = 108) - 20s gill net	15%	NA	To spawning habitat (22 km) Gill net: 28% Gill net + 1 min air exposure: 31% Biopsy: 33%	High risk - Gill net	NA	Present	Bass et al. 2019
Gill net (tangle net)	Sockeye	Escapement Temperature Loose vs. tight gill net	Telemetry ² (N = 385)	NA	14%	Up to ~800 rkm Total: 33% <19°C ⁵ Control: 17% Escape (loose and tight net): 63% >19°C ⁵ Control: 45% Escape (loose and tight net): 77%	Very high risk - >19°C water - Tight gill net - Severe injury (deep and dark net marks, > 20% scale loss)	Moderate risk - <19°C water - Loose gill net - Minor injury (faint net marks, surface wounds, <5% scale loss)	Absent	Reid 2020
	Sockeye	NA	Telemetry ² (N = 130)	NA	NA	From mid-river to ⁵ : ~15 rkm: 12% ~240 rkm: 37% Sub-natal watershed (mean 15 days): 67%	Very high risk	NA	Absent	Donaldson et al. 2010
Beach seine	Coho	NA	Telemetry ¹ (N = 50)	NA	1 hr: 5% 24 hr: 6%	96 hr: 12% Release to sub-natal watershed: 26%	Very high risk - fishery handling time >6min	Moderate risk - fishery handling time <6min	NA	Raby et al. 2012b
	Coho	Temperature	Holding (N = 35)	NA	24hr 2 min Entanglement 10°C: 0% 15°C: 0% 15 min 10°C: 0% 15°C: 18%	NA	Moderate risk - 15min entanglement - 15°C water ⁹	Low risk - 15min entanglement - 10°C water	NA	Raby et al. 2015a
Angling	Sockeye	Exhaustive exercise Air exposure Assisted ventilation	Telemetry ¹ (N = 209) - barbless J-hooks (3/0) - nylon landing net - <2 min handling	NA	NA	72 hr post-release Angling: 13% Angling + air exposure: 14% Angling + air exposure + assisted ventilation: 6% To spawning habitat Angling: 30% Angling + air exposure: 20% Angling + air exposure + assisted ventilation: 29%	High risk ³ - Air exposure	Moderate risk ³ - No air exposure	Present	Robinson et al. 2015
Angling simulation (3min chase + 1 min air exposure)	Sockeye	Exhaustive exercise Air exposure Assisted ventilation	Telemetry ¹ (N = 209)	NA	NA	To spawning habitat ⁷ Total: 83% Control: 60% Simulation: 91% Simulation + assisted ventilation: 97%	High risk	NA	Present	Robinson et al. 2015
	Sockeye	Temperature Exhaustive exercise Air exposure Assisted ventilation	Holding ¹ (15 days, N = 103)	NA	NA	3 days 21°C all treatments: 100% 10 days 16°C Control: 17% Chase + air exposure: 16% Chase + air exposure + assisted ventilation: 26% 15 days 16°C Control: 27% Chase + air exposure: 39% Chase + air exposure + assisted ventilation: 58%	Very high risk - 21°C water - With or without air exposure	Moderate risk - 16°C water - No air exposure	Present	Robinson et al. 2013
	Sockeye	Exhaustive exercise Air exposure	Holding ¹ (N = 101)	NA	NA	72 h ⁷ 13°C: 0% 19°C: 0% 21°C: 10% Handling: 45% Capture: 64% Capture + air exposure: 67%	High risk ³ - 21°C water - Air exposure	Low risk - 13°C water - No air exposure	Present	Gale et al. 2011
Beach seine Angling	Sockeye	Assisted recovery	Telemetry ² (N = 99) - beach seine: 6 min handling time - angling: 1 to 3/0 barbless J hooks, a knotless landing net (3 min mean handling time; air exposure <1 min)	NA	24 h Immediate release: Angling: 3% Beach seine: 4% Beach seine + assisted: 20%	48 h Immediate release: Angling: 22% Beach seine: 9% Beach seine + assisted recovery: 39% To sub-natal watershed Immediate release: Angling: 64% Beach seine: 48% Beach seine + assisted: 97% Baseline ⁶ : 30%	High risk - Beach seine with 24 h assisted recovery in net pen	Moderate risk - Beach seine	NA	Donaldson et al. 2011b

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Table 1 (continued)

		Sockeye	Air exposure Assisted recovery	Telemetry ² (N=173)	NA	NA	To spawning habitat Beach seine: 42% Angling: 69% Angling + air exposure: 71% Angling + recovery: 83% Angling + air exposure + assisted recovery: 50% Baseline ¹⁰ : 30%	High risk - Angling - 1 min air exposure - No assisted recovery	Moderate risk - Beach seine - No assisted recovery	NA	Donaldson et al. 2013
	Angling simulation (3min chase + 1 min air exposure)	Sockeye	Exhaustive exercise Air exposure	Holding ² (N= 106)	NA	NA	48 h Control 13°C: 7% 16°C: 30% 19°C: 33% Chase 13°C: 36% 16°C: 0% 19°C: 40% Chase + air exposure 13°C: 9% 16°C: 30% 19°C: 40%	Very high risk - >18°C water - Equilibrium loss for >2 min - Ventilation frequency >1 breath s ⁻¹	Low risk - 13°C water - No air exposure - Regained equilibrium in <130s - Ventilation frequency >62 breaths min ⁻¹	Present	Gale et al. 2014
Freshwater to terminal tributary	Beach seine Gill net Tangle net	Sockeye	Air exposure	Telemetry ² (N = 116)	Released: 0% Beach seine: 0% Gill net: 7% Tangle net: 7%	NA	5 days post-treatment Released: 21% Beach seine: 32% Gill net: 48% Tangle net: 45% To spawning habitat Released: 72% Beach seine: 68% Gill net: 84% Tangle net: 83%	Very high risk - Gill net and tangle net - Severe injury (score = 1; damage to gills) - Impaired orientation	Moderate risk ³ - Beach seine	NA	Donaldson et al. 2012
		Sockeye	NA	Telemetry ² (N = 214)	- 1min entanglement in either gear	NA	12-15 days Control: 23% Gill net escape: 26% Beach seine escape: 17% Tangle net escape: 8%	Very low risk	NA	Absent	Elmer et al. 2022
		Sockeye	NA	Telemetry ² (N = 629)		NA	2-3 weeks ⁷ Late Shuswap Gill net 48 km: 65% 131 km: 54% 450 km: 25% Beach seine 48 km: 29% 131 km: 38% 450 km: 18% Summer-run Gill net 131 km: 98% Beach seine 131 km: 91%	Very high risk - Gill net - Lower river fishery (early in the migration) - Net injury - Temperature >18°C - Small fork length	Moderate risk - Terminal fishery - No injury - Temperature <16°C	Present	Bass et al. 2018b
Terminal tributary	Gill net Angling	Pink Chum	Air exposure Exhaustive exercise	Monitor in spawning channel ¹ (N = 267)	- Angling treatment involved using a size 1 barbless J hook inserted into the upper jaw	NA	Until natural mortality (duration not provided) All treatments: ~5%	Low mortality - Capture (angling or gill net) - 1 min air exposure	NA	NA	Raby et al. 2013

low risk corresponds to 0–5 % observed RM; moderate risk corresponds to 6–25 % observed RM; high risk corresponds to 26–45 % observed RM; and very high risk corresponds to > 45 % observed RM.

4.1. Marine environment

Anadromous salmon begin their homeward migration in the marine environment, where adult Pacific salmon have loose silver scales, are not reproductively mature, and predominantly inhabit epipelagic coastal and offshore waters (Quinn, 2005). For instance, telemetry research off the BC coast indicated Chinook salmon typically occurred at 30 m depth ($22 \text{ m} \pm 0.36 \text{ m}$; mean \pm SEM), less than 1 % of individuals ventured deeper than 150 m, and average depth decreased as Chinook approached terminal, or estuarine waters (Freshwater et al., 2024; Hendricks, 2024). Marine environmental conditions are relatively consistent compared to estuarine and freshwater environments. As a result, primary environmental pressures in the marine environment include pathogens, parasites (e.g., sea louse, lamprey), and predation by larger fish and marine mammals. In the marine system, Pacific salmon

are targeted predominantly by commercial purse seine, commercial and Indigenous gill net fisheries, and hook and line (i.e., recreational angling, subsistence, personal use, and commercial trolling) fisheries, and caught as bycatch in groundfish trawl fisheries (Fig. 1). Marine fisheries landings are more likely to be comprised of multiple species and genetically distinct populations (e.g., Raby et al., 2015c; Cook et al., 2018a), given that mixing increases with distance from the natal watershed (Beacham et al., 2005). The mixture of genetically distinct populations may increase the variability of RM estimates compared to freshwater fisheries since stress coping mechanisms, vulnerability to injury, and therefore RM rates, may be more similar among fish within a population (Donaldson et al., 2012, 2014; Cook et al., 2018a).

4.1.1. Environmental effects

By inhabiting the marine epipelagic zone, barotrauma and thermal shock are potential factors that may contribute to RM in marine fisheries. Barotrauma in marine fisheries occurs when a fish undergoes rapid depressurization when brought to the surface (discussed in Brown et al., 2014; Cook et al., 2019b). Gasses in the swim bladder expand causing

visible injury such as exophthalmia (a.k.a. bulging eyes) and everted stomachs, as well as tissue damage including ruptured swim bladders and internal haemorrhaging. Risk of mortality due to barotrauma increases with the speed at which the fish are brought to the surface and typically results in long-term and indirect mortality (e.g., reduced foraging, stress, infection risk) (Cook et al., 2019b). However, Pacific salmon vulnerability to barotrauma may be reduced due anatomical traits, such as their physostomous swim bladder where the connection with the stomach facilitates off-gassing (Brown et al., 2014; Ng et al., 2015; Cook et al., 2019b). In fact, recent data shows that Chinook salmon can reach speeds as fast as 1.31 m s^{-1} when moving vertically in the water column, with a typical speed $\leq 0.12 \text{ m s}^{-1}$ (Hendricks, 2024). Few studies have examined barotrauma in Pacific salmon, and those that have focused on juveniles in the context of passing hydro structures (reviewed in Brown et al., 2014). A holding study that exposed lake trout (*Salvelinus namaycush*) to a gill net simulation (mean lake depth 28 m) observed potential indications of barotrauma, such as bloating, difficulty swimming, and hemorrhaging in the eyes, which, in severe cases, coincided with RM (Ng et al., 2015). Additionally, mortality rates were higher for smaller fish, presumably due to greater sensitivity to barotrauma. Yet, it is worth noting that the effects of handling were not considered in that study, which may have contributed to mortality. In contrast, research examining mechanisms of RM in marine angled Chinook and coho salmon have not observed external injuries indicative of barotrauma (i.e., exophthalmia, everted stomachs; E. Lunzmann-Cooke, K. Zinn, S. Johnston, pers. comm.) despite some fish being captured at great depths. Barotrauma was also not mentioned as a dominant mechanism of RM in field studies simulating purse seine capture events involving chum (Cook et al., 2018b), sockeye (Cook et al., 2018a), and coho (Raby et al., 2015; Cook et al., 2019a) salmon. However, examination for more cryptic internal indicators of barotrauma (e.g., ruptured swim bladders, hemorrhaging) was not in the scope of those studies.

Thermal shock can arise when there is an abrupt change in temperature when fish are caught in deep, cold water and brought to the warm surface (Cook et al., 2015; Patterson et al., 2017a). Risk of thermal shock increases with the temperature gradient and can result in immediate or delayed mortality by triggering physiological impairment or decreasing resilience to additional stressors (Donaldson et al., 2008b). Thermal experience at time of capture has been shown to influence mortality outcomes to a greater degree than pre- or post-capture experience (Van Leeuwen et al., 2024). Furthermore, once landed, warm air temperature decreases a fish's tolerance to air exposure by increasing the rate that water evaporates from the gills. As a result, gill filaments adhere to each other quicker than in cooler temperatures and the gill lamellae collapse (Ferguson and Tufts, 1992; Cook et al., 2015; Patterson et al., 2017a). Resulting asphyxiation forces fish to transition to anaerobic respiration and contend with subsequent physiological consequences (e.g., oxygen debt, acidosis, increasing lactate, glucose, and cortisol concentrations).

4.1.2. Net-based fisheries

External injuries caused by marine net-based fisheries, such as scale loss, fin damage, and tissue wounds, can lead to impaired osmoregulation and homeostasis, increase the susceptibility to infection, and decrease swimming performance, acting as potential mechanisms of delayed mortality (Table 1; Tierney and Farrell, 2004; Teffer et al., 2017; Cook et al., 2019a; but see Raby et al., 2015c where mortality could be related to injury in the holding study but not in the telemetry study). In fact, a holding study examining coho salmon recovery for 84 h after a commercial purse seine simulation observed that dermal injuries (assessed according to scale loss, skin loss, wound depth, and fin damage) and reflex impairment were correlated with impaired ion homeostasis (i.e., osmolality, sodium, chloride) and plasma lactate concentrations (Cook et al., 2019a). Survival probability decreased to $< 45\%$ when fish were both impaired (RAMP of 0.4) and injured, but 94 % of individuals that were not impaired or injured survived. Blood

lactate was also deemed a predictor for mortality because elevated levels decrease blood pH potentially causing blood acidosis. Cook et al. (2019a) found that lactate concentrations upon capture increased over time in more severely injured individuals but recovered within 48 h in less injured fish. Similarly, telemetry studies examining coho salmon survival post-release from a purse seine attributed mortality to scale loss and reflex impairment (Raby et al., 2015c; Cook et al., 2018a). Severe scale loss (i.e., $>50\%$ of the body) and body flex impairment corresponded to a 61 % increase in predicted mortality, where survival within the first 43–56 km from release locations (median of 4.6 days) was 86 % for unimpaired and uninjured fish, but 25 % for fish in the worst condition (impaired and severe scale loss; Cook et al., 2018a; Table 1). Severe scale loss also corresponded with longer migration times, but this was not the case for reflex impairment. Hence, there is strong indication that disruption to ion homeostasis caused by dermal injuries, particularly scale loss, prolongs physiological recovery; a likely mechanism underpinning RM. Physiological impairment and heightened infection risk can be especially detrimental early in the spawning migration as it can have lingering effects on fish when they transition from marine to fresh water, where osmoregulation stress is heightened (Cooperman et al., 2010) and fish are exposed to new infectious agents (Bass et al., 2017; Teffer et al., 2021).

Longer entanglement, crowding and sorting times, tighter strung nets, and higher catch densities are all positively related to reflex impairment, and injury (scale loss, tissue scars, fin fraying) and are associated with “high” or “very high risk” mortality (Table 1; Cook et al., 2018a, 2018b [chum, coho]; Reid, 2020 [sockeye]). Together these factors increase the probability that fish become injured from contact with the net, entanglement or crushing, and physiologically impaired from hypoxia and exhaustion from attempting to escape entrapment. Whereas gill and tangle nets are designed to constrict fish, ultimately causing physical injury (Baker and Schindler, 2009; Teffer et al., 2017; Bass et al., 2018a), selecting the appropriate mesh size for purse seine fisheries involves balancing a trade-off between selecting a small mesh size that increases drag (affects fuel costs) versus a large mesh size that gills the target species, increasing injury and handling time to detangle fish (Patterson et al., 2017a). Injuries and reflex impairment from purse seine fisheries worsen over time (especially fin damage) and is generally more extensive in smaller individuals and females (Raby et al., 2015c; Cook et al., 2019a; Reid, 2020), making these groups more susceptible to RM. Furthermore, the longer fish spend in a net, the greater the risk of injury and exhaustion. For instance, a holding study simulating a purse seine fishery showed that increasing the time that chum salmon spent pursed corresponded with elevated lactate ($>11.5 \text{ mmol L}^{-1}$) and chloride concentrations (indicators of exhaustion), reaching a threshold after 15 mins (i.e., potentially reached the limit of anaerobic exercise; Cook et al., 2018b). The same study also showed a positive relationship between RAMP score and time pursed; except when fish were crowded, in which case the degree of reflex impairment was the same regardless of time spent crowded (although it is worth noting that RAMP score was more related to air exposure duration; see next paragraph). In contrast, in a similar study involving coho salmon, Cook et al. (2018a) did not see a relationship between set size (i.e., number of fish caught per net haul) and coho salmon condition or mortality, but this was potentially because injury was mitigated by the use of a brailer.

In gill net fisheries, reducing entanglement duration decreases the probability of mortality from “very high” to “moderate” (Table 1; Buchanan et al., 2002; Teffer et al., 2017). A holding study exposed sockeye salmon to either a 20 sec or 20 min gill net entanglement and observed mortality in both treatment groups (57 % and 76 %, respectively; Teffer et al., 2017; Table 1). Most fish died within 5–7 days post-capture and showed necrosis from fungal infections on the skin, gills, and muscle tissue, matching the locations where gill nets constrict and cause injury (similar injuries have also been related to mortality following gill net encounters elsewhere; e.g., Baker and Schindler, 2009; Bass et al., 2018a) and contained elevated levels of microbes indicative

of enhanced stress, injury, and a compromised immune system. It is worth noting that the Teffer et al. (2017) study collected sockeye salmon during their upriver migration, where the pathogen community differs from marine pathogens (A. Bass, Fisheries and Oceans Canada, pers. comm.). In general, mortality is high after gill net encounters (Table 1; Donaldson et al., 2012; Teffer et al., 2017; Bass et al., 2018a; Elmer et al., 2022). Delayed release mortality was reduced when the fisheries simulations were mild (i.e., short soak time, no injury; e.g., Nguyen et al., 2014), water temperature was less than 18°C, and when sockeye salmon were more mature (Bass et al., 2018b).

Higher catch density increases the risk of exhaustive exercise and longer bouts of air exposure onboard the vessel. Large purse seine catch densities (i.e., number of fish caught per tow) accelerate the depletion of localized oxygen levels in the net or brail (Table 1; Raby et al., 2014a, 2015c; Cook et al., 2018b), and catch density has been correlated to reflex impairment (Raby et al., 2015c). Air exposure during sorting causes asphyxiation and acidosis, made evident by a decrease in blood glucose (indicating depletion of readily useable endogenous energy supply) and an increase in lactic acid concentration as fish shift to anaerobic metabolism (Ferguson and Tufts, 1992; Cook et al., 2015). Physiological effects include reflex impairment, where it only takes one or two impaired reflexes to see survival rates declining (Raby et al., 2012a; Cook et al., 2018b), elevated lactate levels lasting 24–48 h post-handling, and changes in plasma cortisol, glucose, and potassium 24 h post-seine net fisheries interaction (Raby et al., 2015c; Cook et al., 2019a). All these deviations from homeostasis indicate short-term effects of exhaustive exercise post-capture. For instance, air exposure to chum salmon following capture in a purse seine caused glucose levels to decline after 6 mins of air exposure (even dropping below the normal 4–7 mmol/L level necessary to sustain life) and was positively correlated with RAMP scores (Cook et al., 2018b). The probability of mortality became high after 4–5 mins of air exposure (fish were likely to have 3 reflexes impaired; RAMP = 0.6) and death was almost certain after 6 mins air exposure (fish were likely to have 4 reflexes impaired; RAMP > 0.8). Furthermore, cardiovascular performance is affected by air exposure and exhaustive exercise as fish become bradycardic until they are returned to the water, at which point the heart rate becomes tachycardic (Cooke et al., 2001; Raby et al., 2015a; Prystay et al., 2017). Notably, this response may differ if fish were already stressed prior to the capture event (e.g., by high temperature or salinity stress, or, a previous fisheries encounter) such that heart rate is continuously tachycardic (Brijs et al., 2019) which would impact post-release recovery. Increases in oxygen demand to regain homeostasis post-fisheries encounter may have implications on the cardiovascular system's (i.e., aerobic and circulatory) capacity to support other important processes such as swimming and predator avoidance (Lawrence et al., 2023), osmoregulation, growth, and maturation (Brijs et al., 2019; Birnie-Gauvin et al., 2023). Overall, hypoxia thresholds and recovery time depend on environmental conditions (e.g., temperature), individual traits (e.g., size, species), sex, and life stage, and become exacerbated by injury and handling duration (Cook et al., 2015).

4.1.3. Hook and line fisheries

Marine hook and line fisheries include commercial troll fisheries and recreational angling. Similar to net-based fisheries, injury characterised by severe bleeding, scale loss, and eye damage correspond to an increase in RM risk from “low risk” to “very high risk” in marine recreational fisheries (Table 1; Hinch et al., 2024; Lunzmann-Cooke et al., 2024). Smaller individuals are more prone to injury, where wound location, such as hooking the gills, and bleeding are typically associated with quicker mortality (Hinch et al., 2024). Severe injury can be caused by deep hooking as it increases bleeding and risks puncturing vital organs, such as the liver or gills (Gjernes et al., 1993; Schill, 1996). Barbed hooks increase the risk of severe bleeding and handling (DuBois and Pleski, 2007) and therefore presumably increase the risk of RM. The use of bait which is commonly used in commercial and recreational trolling does

not increase the probability of deep hooking (Johnston et al., 2021), which is likely a result of the active trolling nature of marine recreational fisheries where the boat speed reduces the possibility of swallowing the bait or lure. Indeed, for other fishes, passive use of bait is typically associated with deep hooking (Arlinghaus et al., 2007). Cutting the line when deep hooking occurs has been found to reduce the risk of mortality, rather than struggling to remove the hook, which extends air exposure and handling time and likely increases injury severity (Schisler and Bergersen, 1996; Tsuboi et al., 2006; Cooke and Danylchuk, 2020).

Hook and line related injuries can result in severe bleeding, bruising (if dropped on the boat's deck), and scale loss which all can have a delayed effect on mortality (Hinch et al., 2024 [Chinook]; Lunzmann-Cooke et al., 2024 [coho]). Eye injuries are also common as hooks can penetrate the eye from inside the fish's mouth and fish have limited recovery capacity from these injuries resulting in persisting sublethal effects and delayed mortality (15–20 % mortality in Chinook salmon, Table 1; Wertheimer, 1988; Hinch et al., 2024; Lunzmann-Cooke et al., 2024). For example, the odds of RM were 2.8 times greater in coho salmon that incurred an eye injury during recreational marine angling compared to fish in good physical condition or that did not have an eye injury (Lunzmann-Cooke et al., 2024). The type and severity of injury often depends on the hook type and angler experience. Treble hooks are more likely to hook the inner mouth and to be swallowed compared to single hooks, resulting in more flesh puncture wounds, and require longer air exposure and handling times for dehooking (DuBois and Dubielzig, 2004). Holding study research also shows that smaller Chinook (fork length < 60 cm) have 29 % lower survival rates when caught on a treble hook compared to a single hook (Table 1; Hinch et al., 2024). Nevertheless, the probability of causing eye injury increases when using a single hook. For single hooks, larger hook size relative to mouth size typically increases the likelihood and severity of an injury occurring, as the larger gauge (thickness) of the hook is more impactful upon penetration and the larger gap between the point and the shank promotes posterior eye-hooking injuries to occur (DuBois and Pleski, 2007; Chiaramonte and Meyer, 2021; Hinch et al., 2024). However, hooks that are particularly small are prone to expulsion during capture leading to injuries and unobserved escape-related mortality. Notably, a recent telemetry study experimentally testing the effects of trolling on coho salmon did not observe differences in injury frequency or severity between 3/0 and 5/0 hook sizes (octopus and J hooks), presumably because 3/0 hooks are already large relative to the mouth size of coho, making fish prone to injury even at the smallest hook size tested and the difference in gap-width (16 mm and 18 mm, respectively) was relatively small (Hinch et al., 2024). In a different study, RM was higher if coho salmon exhibited scale loss, eye damage, or bleeding, and was skewed toward smaller individuals (31.5 % RM after 3.3 days (median); Table 1; Lunzmann-Cooke et al., 2024). Hence, when it comes to marine hook-and-line fisheries, larger fish appear to have a higher probability of survival than smaller individuals when released, yet smaller individuals are most likely to be released by anglers in their quest to obtain their daily limits with larger bodied fish.

Bringing fish onboard increases the risk of RM compared to waterline releases. Studies have shown an interactive effect of air exposure and warm water temperature negatively affect swimming ability, survival, reproduction, and cause physiological disturbance to salmonids caught in freshwater systems (Gale et al., 2011; Richard et al., 2013; Twardek et al., 2019). In marine settings, air exposure duration is not as strong a factor of RM (Hinch et al., 2024) possibly because water temperatures are typically much cooler facilitating post-release recovery. Indeed, marine purse seine studies found that air exposure contributed to RM in chum (Cook et al., 2018b) and coho, however, fish in these studies were left air exposed on sorting tables of the deck (common practice in purse seine fisheries) rather than handled comparatively quicker and under control in a net (as seen in angling fisheries). On deck, fish are more likely to be injured by trauma or rubbing against one another and the boat surface, exposed to air for longer periods than in an angling event,

and spend more energy thrashing. These findings indicate that for marine angling, the risk of mortality or of sublethal effects increases due to the actions associated with air exposure (i.e., capture and handling) rather than air exposure duration alone (Lamansky and Meyer, 2016; Hinch et al., 2024; Lunzmann-Cooke et al., 2024).

Handling capture fish during angling often involves the use of a net, which causes fin damage, mucus loss and scale loss. The severity of these outcomes is related to net mesh size (i.e., more fin damage with larger mesh size; Lizée et al., 2018 [brook trout (*Salvelinus fontinalis*)]; Moltumyr et al., 2022 [Atlantic salmon (*Salmo salar*)]) and material, where rubber knotless nets cause less severe abrasive damage than knotted nets (Barthel et al., 2003; Hinch et al., 2006; Lizée et al., 2018; Philipp et al., 2023). Furthermore, larger coho salmon appear to be more vulnerable than smaller ones to fin damage from landing nets (Hinch et al., 2024). A holding study revealed that the number of damaged fins was directly correlated with levels of Chinook salmon mortality. A recent marine telemetry study found a strong relationship between the number of fins damaged and RM of Chinook salmon to reach spawning grounds, presumably because fin damage affects swimming performance and migration upstream (Hinch et al., 2024; Table 1). Although landing nets can injure Pacific salmon, handling fish without them by just using wet hands increases the likelihood of fish being dropped on deck or on land (Lizée et al., 2018). Post-release survival can be reduced from “very high risk” to “low risk” by not landing the fish, but instead dehooking them at the water-line (Table 1). Purpose built tools can be used for this which has been shown to limit fin damage, scale loss, and air exposure (Hinch et al., 2024).

4.2. Estuarine and lower river

For homing anadromous salmon, the estuarine environment is the transition zone between the marine feeding habitat and the sometimes long (i.e., hundreds of kilometres) freshwater migration to spawn. This transition from slow oceanic and tidal currents to fast flowing rivers can coincide with shifts from cold saline water to warmer fresh water. Crossing the salinity gradient represents a hurdle that Pacific salmon must contend with during their homing migration (Shrimpton et al., 2005; Miller et al., 2009; Cooperman et al., 2010; Hinch et al., 2012). This transition has been examined in an experimental study on adult sockeye salmon captured from the Strait of Georgia, BC (Cooperman et al., 2010) in which individuals were subjected to one of three salinity treatments (fresh water, saltwater, or an intermediary salinity) and half of the individuals in each treatment were injected with gonadotropin-releasing hormone to accelerate maturation. Fish were held in each treatment for one week before collecting gill and blood plasma samples. Mortality was roughly two-fold greater for more sexually mature fish exposed to saltwater compared to individuals that were exposed to fresh water regardless of maturation. Downregulation of Na^+ , K^+ , and ATPase activity causes individuals to progressively lose their saltwater tolerance such that by the time fish reach fresh water they are physiologically adapted to the low salinity (hypo-osmotic) environment (Shrimpton et al., 2005). Whereas transformations to the gills, gut, and kidney enable Pacific salmon to survive in fresh water, it also means that once fish are prepared for fresh water, they cannot tolerate any additional stress in salt water (Cooperman et al., 2010). The authors estimated fish sensitivity lasts 4–6 days, starting when fish are in salt water and ending after fish have transited into fresh water. Hence, RM risk increases if individuals prolong their exposure to salt water, which may occur if the fisheries interaction causes physiological stress requiring recovery during this period of sensitivity, if fish are not released in the same salinity environment as where they were caught, or if the fisheries interaction substantially reduces an individual's osmoregulatory capacity (e.g., due to injury such as scale loss) (Cooperman et al., 2010; Hruska et al., 2010).

In addition to remodelling gill and kidney function to maintain osmoregulation, fish begin to undergo physiological and physical

transformations in preparation for spawning. Their epidermis begins to thicken, scales begin to be reabsorbed, and their gonadosomatic index (GSI) increases. Migrating Pacific salmon cease feeding, leaving them with finite endogenous energy reserves to fuel migration, overcome physical obstacles (e.g., fishways, dams, predators), develop reproductive organs and secondary sexual characteristics, and spawn (Crossin et al., 2004; Hendry and Berg, 1999; Hruska et al., 2010). Fasting also leaves homeward migrating Pacific salmon with limited metabolic scope to recover from stress and injury (Fig. 1), where disproportionately high energy use during migration may result in failed migration or pre-spawn mortality (Rand and Hinch, 1998; Crossin et al., 2009). The exact point at which fish cease feeding along the migration trajectory varies depending on the population (Morash et al., 2013; Quinn, 2005) and likely across years.

Water temperatures are increasing with climate change, altering the environment that Pacific salmon inhabit during their spawning migration (Mote et al., 2003; Martins et al., 2011; DFO, 2023c). For instance, the hydrology in the Fraser River – a major Pacific salmon migration river in British Columbia – is dominated by precipitation and snowmelt (Stewart et al., 2005). Annual peak flow typically occurs in the spring and early summer as the snow melts; discharge then declines as the summer progresses and the snowpack disappears. The summer water temperature of the Fraser River has been increasing by 0.33°C per decade since the 1950's due to earlier snowmelt and increasing atmospheric temperature (Patterson et al., 2007; Hinch and Martins, 2011). Given the strong influence of snowmelt on the hydrology, sockeye salmon that migrate earlier in the summer are not exposed to as warm water temperatures as late-summer run populations but face higher discharge levels (Patterson et al., 2007). In contrast, late-run sockeye salmon stocks have been recorded entering the Fraser River 3–6 weeks earlier than usual (Hinch and Martins, 2011; Hinch et al., 2012). This behaviour prolongs their freshwater residence time, where they are still exposed to warmer than usual water temperatures ($\sim 5^\circ\text{C}$ above historical temperatures). Research on sockeye salmon revealed that there are population-specific thermal tolerance thresholds (Eliason et al., 2011), indicating that some populations are less susceptible to thermal stress than others. A recent review has noted that population, and life-stage specific thermal tolerance actually exists in several Pacific salmon species (Mayer et al., 2024). Thermal stress is an escalating issue as it inhibits an individual's capacity to cope and recover from additional stress, such as fisheries related stress, and enhances pathogen propagation, which can accelerate disease progression (see section *Pathogens and disease*).

In estuarine environments, Pacific salmon are targeted by commercial and Indigenous gill net and beach seine fisheries, and by recreational anglers. Pacific salmon populations with longer migrations are hypothesized to be better at coping with capture stress at the river entry, as survival rates have been shown to be higher in populations spawning farther from the ocean (Donaldson et al., 2010; Cook et al., 2018a). Consistently, Pacific salmon with long fresh water migrations start them with high density of gross somatic energy (Crossin et al., 2004; Bass et al., 2018a; Elmer et al., 2022) and are more energy efficient when facing migratory challenges (Crossin et al., 2004; Eliason et al., 2011; Bowerman et al., 2017; Cook et al., 2018a). For instance, Donaldson et al. (2010) tagged sockeye salmon near the Fraser River mouth and found that Adams-Shuswap individuals (~ 480 river km migration) had slower migration rates and much lower migration success than Chilko individuals (~ 630 km migration) enroute to sub-natal watersheds (77 % vs. 57 %, en-route mortality respectively). Differential mortality was attributed to how these populations coped with metabolic and osmoregulatory impairments. Together, the cumulative environmental effects (i.e., osmoregulation, temperature, and disease) and biological context of the estuarine phase of the migration influence the fish's stress response (Crossin et al., 2008; Gale et al., 2013; Bass et al., 2019; Teffer et al., 2019).

4.2.1. Sex-specific differences

Upon entering fresh water, female Pacific salmon have markedly higher mortality rates compared to males when exposed to stressful conditions (Crossin et al., 2008; Jeffries et al., 2012; Bass et al., 2019; Fig. 1). A recent meta-analysis revealed mortality was 2–8-fold greater in females than males (e.g., male mortality = 10 % and female mortality = 80 %) during their homing migration when environmental conditions were challenging (e.g., high water temperatures, high discharge; Hinch et al., 2021). This phenomenon was particularly apparent during fisheries interactions when coupled with a major secondary stressor, such as increasing temperature (Table 1; Martins et al., 2012; Gale et al., 2014; Eliason et al., 2020). For instance, 48-hour mortality of sockeye salmon exposed to three minutes of exhaustive exercise followed by one minute air exposure was 12 % for females and 6 % for males at 13°C, 20 % for females and 10 % for males at 16°C, and 40 % for females and 20 % for males at 19°C (Gale et al., 2014). Exact causes for elevated female mortality rates remain poorly understood (reviewed in Hinch et al., 2021) however, one leading hypothesis is that mortality is driven by the heightened oxygen demands of female gonads reducing aerobic scope (i.e., capacity to cope with and recover from additional stressors or spawning behaviours, such as temperature stress, swimming, or fisheries interactions). Mature female gonadosomatic index (GSI) is 16–24 % where the ovaries use almost 50 % of female GSE stores – compared to a GSI of 3–5 % in males – and much of the development occurs during the spawning migration (Crossin et al., 2004). Indications of cardiac oxygen limitations (Clark et al., 2009; Sandblom et al., 2009; Eliason et al., 2020) and reduced aerobic scope compared to males (Clark et al., 2011), along with other indications of heightened physiological disruptions in response to stress (e.g., plasma ions, lactate, reflex impairment; Gale et al., 2014) have been observed in mature female Pacific salmon across several studies. For instance, mature female sockeye salmon exposed to a mild beach seine simulation and tagging showed greater physiological stress compared to males, reflected by elevated plasma ions, glucose, and lactate levels, elevated ventricle lactate levels, and a four-hour delayed recovery compared to males (Eliason et al., 2020). However, a study monitoring post-exhaustive exercise recovery in coho salmon did not find any evidence of sex-specific differences in recovery (Kraskura et al., 2020). Yet, this study was conducted in the late fall when water temperatures were quite cool. Other sex-specific physiological and behavioural differences may also explain or contribute to enhanced female mortality, such as elevated baseline cortisol levels (Cook et al., 2011; Gale et al., 2014) and heavy reliance on anaerobic metabolism to overcome physical barriers (Burnett et al., 2014), both of which can inhibit metabolic recovery and contribute to energy exhaustion after fisheries induced stress (Milligan, 1996; discussed in Hinch et al., 2021). In general, sex-specific differences are most acute in the freshwater stages of the spawning migration (e.g., Crossin et al., 2007; Cooperman et al., 2010; Lunzmann-Cooke et al., 2024), presumably because Pacific salmon caught in fresh water are more sexually mature and water temperatures in the summer are substantially warmer than in marine areas.

4.2.2. Environmental effects

4.2.2.1. Temperature. Indubitably, RM can be exacerbated by temperatures that are elevated beyond metabolically optimal levels (Muoneke and Childress, 1994; Martins et al., 2011; Jeffries et al., 2012; Gale et al., 2013; Van Leeuwen et al., 2020; Teffer et al., 2021; Keefe et al., 2022). For instance, a holding study that exposed sockeye salmon to a fisheries simulation (3 min chase, 1 min air exposure, and assisted ventilation) at 16°C or 21°C had a marked difference in survival based on temperature treatment (Table 1; Robinson et al., 2013). Twenty percent of the male sockeye salmon from the 16°C treatment died, with mortality beginning 4 days post-treatment; whereas 100 % of sockeye salmon exposed to the fisheries simulation at 21°C died within 3 days. Similarly, predictive

modelling estimated Atlantic salmon mortality after a recreational angling event increased from less than 5 % in 12°C water to as high as 33 % in 18–20°C water (Van Leeuwen et al., 2020). Fish have thermal tolerance thresholds, where temperatures beyond optimal elicits physiological stress, reduces cardiovascular performance and aerobic scope (i.e., capacity to withstand additional stressors), and, stimulates burst swimming activity, rapid ventilation, and loss of equilibrium – all of these factors enhance the likelihood of RM (Fry et al., 1947; Farrell, 1997; Crossin et al., 2008; Gale et al., 2011; Eliason et al., 2013a). Warm water temperatures also increase the risk of disease and pathogen infection (Altizer et al., 2013; Teffer et al., 2018, 2019), as well as decrease sex hormone levels (Jeffries et al., 2012; Kraskura et al., 2020; Little et al., 2020), which can delay maturation.

The effects of warming temperatures on fish mortality can reflect a 'knife edge' with just a small eclipse of thermal optima leading to high levels of RM. For example, the upper limit of the thermal optima for sockeye salmon is ~18–19°C (Eliason et al., 2011; Martins et al., 2011). After being released from an experimental gill net at > 19°C, sockeye salmon survival decreased by 25 % for the Chilko stock, 37.5 % for the Late Stuart stock, and 53 % for the Stellako stock (Reid, 2020). The lower mortality rate of Chilko salmon is likely due to the higher thermal tolerance of that population (Eliason et al., 2011; Reid, 2020). Correspondingly, a recent study found that coho salmon held in 18°C had smaller gonads and liver [females only] and a larger spleen than their counterparts exposed to a cooler temperature (9°C) (Little et al., 2020). The combined effects of warm river temperature and maturation-induced physiological and morphological changes seem to compound stress and account for reduced reproductive fitness and delayed mortality in fish released from gear (Donaldson et al., 2010; Martins et al., 2011).

The addition of fisheries stress as a secondary stressor narrows the thermal optimal range in which fish can recover and survive (Gale et al., 2013). Simulated capture and release events of sockeye salmon have repeatedly shown that the impacts of oxygen deprivation, equilibrium loss, and physiological responses that come from exhaustive exercise, asphyxiation, air exposure, and handling (e.g., heart rate, lactate, cortisol) worsen when fish are in warmer water (Gale et al., 2011, 2013, 2014; Robinson et al., 2013; Prystay et al., 2017; Kraskura et al., 2020). These impacts occur across all fisheries, require greater recovery effort or prolonged recovery, and correspond to higher rates of RM (Table 1). Warm temperatures also alter post-release behaviour, where fish will sometimes thermoregulate by holding in cool water post-escapement or release from fishing gear to facilitate recovery (Frechette et al., 2018; Elmer et al., 2022, 2023). This altered behaviour is hypothesized to serve as an energy saving strategy to offset the extra energy spent to escape and to mitigate the negative effects of infections. In fact, a recent study on sockeye salmon found that individuals showed a decrease in thermal stress gene expression following lake migration, where the water was cooler than river temperatures (Elmer et al., 2023). However, holding in cooler water can delay fish migration completion and cause fish to aggregate (Frechette et al., 2018), which in turn may increase their exposure to additional mortality agents, such as osmoregulatory stress if holding in estuarine environments (Cooperman et al., 2010), predation (Wright et al., 2007), recapture in other fishing gear, or increased exposure to pathogens (Miller et al., 2014) (Fig. 1).

4.2.2.2. Pathogens and disease. The transition from marine to freshwater environments coincides with a shift in pathogen community composition, such that pathogen abundance and diversity in the host rapidly increases upon freshwater entry (Bass et al., 2017; Tucker et al., 2018; Teffer et al., 2021; Fig. 1). Chronic high temperature exposure promotes pathogen replication and virulence in many infectious agents (Jeffries et al., 2012; Altizer et al., 2013). Meanwhile, fisheries-related handling and injuries serve as a point of entry for infectious agents, increasing pathogen loads (Baker and Schindler, 2009; Teffer et al.,

2017; Di Cicco et al., 2023) and physiological disruptions from fisheries-induced stress (e.g., osmoregulatory and hormonal disturbances), which facilitate less prevalent agents to infect the host, increasing pathogen diversity and infection intensity (Teffer et al., 2018). Together, these factors, along with physical and physiological changes that come with entering fresh water, contribute to accelerated infection rates, which can reduce longevity, delay migrations, and reduce migration success (Teffer et al., 2017 [sockeye]; 2018 [Chinook]; 2019 [coho]; 2021 [sockeye]; Bass et al., 2019 [Chinook]). For instance, within days of being angled from the marine environment and monitored via a holding study, Chinook salmon which had *Tenacibaculum dicentrarchi*, a naturally occurring pathogen, presented skin ulcers manifesting where fish had been injured or handled (i.e., the caudal peduncle, fins, belly, trunk, and mouth) (De Cicco et al., 2023). Infected fish were also lethargic and exhibited loss of balance and abnormal swimming behaviour. A gill net study found Chinook salmon migratory fate was best predicted by sex and pathogen infection levels rather than the gill net encounter itself (28–31 % RM; but fish were also < 22 km from spawning habitat; Bass et al., 2019; Table 1). In this case, the blood born pathogen *Cryptobia salmositica* was negatively related to the probability of fish reaching spawning grounds. Similarly, sockeye salmon mortality (76 %) following gill net entanglement and 1 min of air exposure corresponded with signs of necrosis on the skin, gill, and muscle tissues, and fungal infections on the gill net injuries (Teffer et al., 2017; Table 1). Although survival was independent of pathogen richness (i.e., number of species of microbes present), immune biomarkers and blood properties at death varied depending on the microbe community and composition, which in turn was related to fish longevity. For Chinook, sockeye, and coho salmon migrating upriver, decreased survival and altered behaviour have been associated with enhanced indicators of stress (e.g., osmoregulation impairment and elevated lactate levels), injury, and upregulation of genes linked to wound healing, inflammation, and bacterial defense (e.g., MMP13, Mx; Bass et al., 2019; Teffer et al., 2017, 2018, 2019). Sex-specific differences in infectious loads and intensity are often correlated with earlier mortality (Bass et al., 2017, 2019), where female mortality is often more than double that of males (e.g., no females infected with *C. salmositica* arrived at the spawning grounds while 58 % of males did; Bass et al., 2019), potentially due to compromised immunoregulation in females (Teffer et al., 2017, 2019 [coho]). Together, these findings provide compelling evidence that infectious diseases contribute to mechanisms driving RM by altering fish physiology and behaviour, which is facilitated by fisheries-related injuries, physiological stress, and warm temperature in fresh waters.

4.2.3. Fisheries-specific effects

4.2.3.1. Net-based fisheries. Injury remains a driving mechanism for RM in brackish and freshwater net fisheries (Nguyen et al., 2014; Bass et al., 2018a; Fig. 1). Gill net injuries manifest in the same manner as those acquired in marine environments, including net marks on the skin, descaling, and abrasion behind the gills and on the head. Simulations examining effects of gill net entanglement duration, air exposure, and injury on sockeye salmon early in their river migration found injury corresponded with higher mortality rates, where only a 30 sec entanglement period was sufficient to increase mortality by 14.5 % (Nguyen et al., 2014; Table 1). It is also worth noting that, in this case, the effect of gill net injury on survival was not related to RAMP, and heightened mortality was only apparent later in the migration (i.e., the effects were slow to develop), despite fish displaying slower initial migration rates post-injury. The delayed effects of gill net injury on survival is likely because injury facilitates infection which requires time before establishing and affecting the fish (Nguyen et al., 2014; Teffer et al., 2017; Bass et al., 2018b). Chronic stress, such as elevated temperature can delay healing and act synergistically with dermal injury to produce latent effects from exhaustion-related stress (discussed in Barton, 2002;

Bass et al., 2018a; Teffer et al., 2021). Pacific salmon are less likely to recover from gill net injuries inflicted earlier in the migration and estimated to have a 16 % higher relative probability of dying en-route compared to uninjured individuals (e.g., 1.16 x baseline mortality; Bass et al., 2018a).

Risk of injury leading to RM varies according to several biotic factors such as sex, maturity, and the location of injury. The estuarine and early river portions of the migration often include a mixture of populations at different levels of maturation, where maturation associated with fresh water residence decreases the risk of severe injury because fish have a thicker epidermis and their scales are less loose, if not already reabsorbed (Bass et al., 2018b). Notably, females and smaller individuals appear more susceptible to gill net injury during their en-route migration; however, this could be because larger males are more likely to be retained by gill nets (Bass et al., 2018a; Kanigan et al., 2019). For example, a three-year telemetry study that intercepted sockeye salmon along their migration calculated the annual gill net injury in migrating Fraser River Gates Creek sockeye salmon to be 21–29 % for females and 13–22 % in males, and males were significantly larger than females (Bass et al., 2018a).

Hypoxia induced by net-based fisheries in brackish and lower river environments causes sub-lethal effects, such as elevated plasma osmolality, lactate, and cortisol levels compared to baseline, and reflex impairment (Nguyen et al., 2014; Raby et al., 2015d). This can affect an individual's ability to resume migration, thereby risking an increase to their exposure to osmoregulatory stress when released in the estuarine environment (Fig. 1; Cooperman et al., 2010). A telemetry study examining coho salmon released from a beach seine in the lower Fraser River observed Pacific salmon experiencing physiological stress characteristic of exhaustive exercise and hypoxia (Raby et al., 2012a), including plasma lactate levels reaching an impairment, and possibly survival, threshold of 10–13 mmol L⁻¹ (Farrell et al., 1998). Longer entanglement duration in a beach seine correlated with depleted localized oxygen levels, higher blood cortisol and lactate concentrations, and fish with greater reflex impairment (RAMP score) prior to release were more likely to experience migration failure (Raby et al., 2012a, 2014a). For example, when water was 15–16°C, oxygen levels in a crowded beach seine decreased by 56–60 % within 10 mins of sorting. In cases where the beach seine tow was not crowded, fish were pulled higher onshore to facilitate sorting, which air exposed the catch. Consequently, Raby et al. (2014a) estimated coho salmon RM to be 3 % upon capture, 19 % within the subsequent 48 h, and 39 % from capture to spawning grounds (Table 1). Although hypoxia is a significant stressor for fish (Cook et al., 2015), several studies indicate Pacific salmon are able to recover from acute air exposure (<2 min) in fresh water at low water temperatures (e.g., Schreer et al., 2005; Gale et al., 2011, 2014; Nguyen et al., 2014).

4.2.3.2. Hook and line fisheries. Major bleeding, eye injury, and use of a landing net continue to negatively affect post-release survival in estuarine and early segments of the freshwater migration. The physiological response to angling is worsened in warmer temperatures, including greater plasma cortisol and lactate levels, immediate but short-term reduction in ATP and phosphocreatine stores, and near depletion of glycogen stores (Meka and McCormick, 2005; Robinson et al., 2013). However, larger fish exhibit greater physiological stress, specifically increased plasma cortisol and lactate levels, which correlate with longer capture and handling durations and warmer temperatures (Meka and McCormick, 2005). Subsequent recovery time and effort after capture increases the risk of fallback, alter migration patterns (e.g., reduce distance travelled), and impact the fish's ability to cross barriers and obstacles, such as dams (Lennox et al., 2015; Havn et al., 2015).

Tackle type (i.e., bait, hook type) and handling have a significant effect on Pacific salmon post-release survival in estuarine and early segments of freshwater migrations. Circle hooks are rounded hooks with

the point facing the shank, leaving the point less exposed compared to J-hooks (Cooke and Suski, 2004). Studies conducted in flowing water systems found that using circle hooks consistently reduce deep hooking in trout when fishing with bait compared to J-hooks (Sullivan et al., 2013; High and Meyer, 2014). This was also the case in a commercial trolling study, where circle hooks caught Chinook salmon by the mouth more frequently than J-hooks (Orsi et al., 1993). But it is also worth noting that circle hooks may not reduce the risk of deep hooking in lentic settings, depends on fishing style, and feeding methods of different species, reinforcing the notion that gear recommendations should be location and target species specific (Grover et al., 2002; Cooke and Suski, 2004; Chiaramonte and Meyer, 2021). During handling, scale loss and fin damage from using a dip-net persists in the estuarine system but the magnitude of scale loss is reduced the longer adult Pacific salmon migrate in fresh water as they begin to reabsorb their scales.

4.2.4. Fallback and delayed migration

Following capture and release in lower river fisheries, Pacific salmon often exhibit downstream migrations (i.e., fallback) that delay, and in some cases fully prevent, subsequent upstream spawning migrations (Bernard et al., 1999; Mäkinen et al., 2000; Liedke et al., 2014; Robinson et al., 2015; Havn et al., 2015; Reid, 2020). Post-release fallback varies by species (e.g., telemetry study showed 21–26 % of Chinook vs. 14 % of coho salmon were likely to fallback < 24 h after release; Liedke et al., 2014), handling and gear (Mäkinen et al., 2000), fish size (Havn et al., 2015; but see Bernard et al., 1999), and environmental conditions (Havn et al., 2015). One study reported that Atlantic salmon swam further downstream post-release from gill nets (mean = 18.1 km) compared to post-release from angling (mean = 2.3 km) (Mäkinen et al., 2000), and the extent of Atlantic salmon fallback has been shown to increase with temperature and decrease with fish size (Havn et al., 2015). However, the mechanisms underlying post-release fallback remain speculative, with injury, stress, and exhaustion often listed as likely culprits. Although, some studies have indicated that injury may be less likely of a mechanism given the studies specifically applied capture and handling techniques aimed to reduce injury risk (Mäkinen et al., 2000; Lennox et al., 2016). It is also possible that downstream migrations are a natural migratory behaviour that reflects initial mistakes by Pacific salmon in attempting to home to natal rivers (Keefe and Caudill, 2014; Havn et al., 2015), which has been observed in non-fisheries captured Chinook salmon (Keefer et al., 2006; Keefer and Caudill, 2014).

Although reduced migration speed may not directly increase RM (Bass et al., 2018a; Elmer et al., 2022; but see Nguyen et al., 2014), it can increase exposure to potentially unfavourable environmental conditions and pathogens. For instance, telemetry research found sex and infection to be the best predictor of migratory fate of Chinook salmon, rather than the gill net encounter itself (Bass et al., 2019). Longevity of Chinook salmon infected with a blood born pathogen was half the longevity of non-infected fish (7 days vs. 14 days, respectively) and males were also five times more likely to complete the migration than females.

4.3. Upper river and terminal areas

In upper river and terminal lakes and streams, climate change is exposing Pacific salmon that migrate in the summer to much warmer temperatures than historically experienced and in many situations now exceeds the upper thermal tolerance of some populations (Hinch et al., 2012; Martins et al., 2012). Lakes and tributaries can provide thermal refuge from warm river conditions where Pacific salmon may seek out intermediate temperature habitats to avoid exhaustion and optimise reproductive development (Gonia et al., 2006; Roscoe et al., 2010; Minke-Martin et al., 2018). However, as climates continue to change causing earlier snow and ice melt, lakes are also warming earlier and faster and becoming less stratified which may eventually limit the availability of these refuge habitats (Hinch and Martins, 2011; Martins et al., 2012; Fig. 1). By the time Pacific salmon approach spawning

regions, they have expended 60–80 % of their endogenous energy reserves (Crossin et al., 2004) and are sexually mature, with developed gonads and secondary sexual characteristics. At this point, semelparous Pacific salmon are also senescing, which encompasses physiological changes including elevated lactate and cortisol levels, decreased plasma ion concentrations and osmolality, and an increasingly limited metabolic scope (Hruska et al., 2010). Therefore, any remaining energy will be necessary to fuel mate competition and reproduction, leaving limited energy to contend with additional biotic and abiotic pressures (Crossin et al., 2004).

Long-term effects of fisheries-related interactions experienced earlier in the marine or lower river environments may contribute to mortality closer to spawning areas (Bass et al., 2018a). For instance, a tagging study examining changes in injury status within the final 45 km of sockeye salmon spawning migration observed a positive correlation between female pre-spawn mortality and individuals that accrued higher migration-related injuries prior to the final leg of their migration (Philipp et al., 2023). A telemetry study targeting Fraser River Gates Creek sockeye salmon with visible injuries indicative of escaping downriver gill nets, and monitoring their migration in the final 45 km of their 380 km spawning migration, found that only 18 % and 16 % of the tagged individuals successfully reached spawning grounds or spawned [females only], respectively (Bass et al., 2018a). As senescence progresses, immunosuppressive hormones are released and the ability of mature Pacific salmon to fight infections deteriorates (Miller et al., 2014), leaving individuals more vulnerable to infections and disease from fisheries injuries accrued earlier in their marine or estuarine migration (Fig. 1) – a captured fish may have been captured and released (or escaped from gear) previously (even multiple times), potentially biasing estimates of unique discards (Runde et al., 2020). This risk is not unique to later stages of the migration but may be higher given the cumulative gauntlet of fishing gear Pacific salmon contend with prior to reaching the spawning grounds.

Indigenous gill net, beach seine, and dipnet fisheries as well as recreational, subsistence, and personal use angling takes place throughout the Pacific salmon freshwater migration (Fig. 1). Despite the deteriorating condition of mature Pacific salmon, RM is usually considerably lower when fisheries occur closer to spawning areas (i.e., terminal fisheries), and increasing evidence indicates Pacific salmon resilience to fisheries stress improves with reproductive maturity (Donaldson et al., 2012; Raby et al., 2013; Bass et al., 2018b). This is especially apparent in a recent telemetry study that reported the mortality rate of sockeye salmon exposed to either gill net or beach seine entanglements occurring at 10 %, 26 %, and 72 % along their 500 km migration to be 65 %, 54 %, and 25 %, respectively for gill net (i.e., double the early migration mortality rate) and 39 %, 38 %, and 18 %, respectively for beach seine (Bass et al., 2018b; Table 1). Furthermore, Bass et al. (2018b) observed higher RM and slower migration rates for sockeye salmon released from gill nets (54–65 %) compared to beach seine (29–38 %), except when sockeye salmon were near the spawning ground, at which point post-release mortality was comparable between the two gears (10 % difference) and gill netted fish migrated to the spawning grounds faster (Table 1; Bass et al., 2018b; Elmer et al., 2022).

Numerous hypotheses have been proposed to explain Pacific salmon's increased resilience to negative aspects of capture and release in upper areas of the freshwater migration. First, fisheries interactions are late enough in the life history that there is insufficient time for delayed effects to manifest and impact migratory fate prior to natural death (Donaldson et al., 2010, 2012). Second, survival could be assisted by less stressful hydrological conditions near spawning areas as up-river flows would be lower, and fish may access lakes which have slow moving water and thermal refugia (Elmer et al., 2022). Third, by late stages of their migration, Pacific salmon have almost fully developed secondary sexual characteristics and undergone physiological transformations that together make capture stress less significant. Among these transformations includes thicker skin by reabsorbing the scales and elevated

baseline cortisol levels (Baker and Vynne, 2014; Hruska et al., 2010; Robertson and Wexler, 1960). The thick skin reduces the likelihood of their skin rupturing during a fisheries encounter, as observed for both gill nets and beach seines (Bass et al., 2018b; Elmer et al., 2022), and the elevated baseline cortisol levels reduce the amount that cortisol would deviate from baseline levels in response to a fishing interaction, attenuating the stress response (Raby et al., 2013). Similar trends have been observed in Atlantic salmon where angling-induced physiological disturbance and mortality was greater for pre-spawned individuals (i.e., bright salmon) compared to post-spawned Atlantic salmon (i.e., kelts) (Brobbe et al., 1996).

Examining the fish response to fisheries interactions at the molecular scale can further elucidate tissue- or cellular-level mechanisms underpinning RM (DePasquale et al., 2023). Yet, such studies are limited in most environments. Donaldson et al. (2014) showed that the expression of genes linked to the endocrine stress response (i.e., JUNB) increased after a fisheries simulation (3 min chase and 1 min air exposure), requiring 24 h to recover. Another study that examined angling-related consequences (fight time <60 s; air exposure < 258 s) on gill functioning at the molecular level found limited evidence that angling impacts the short-term (48 h) molecular response in lake trout (DePasquale et al., 2023). Specifically, gill derived mRNA transcripts indicated angling triggered a cytoprotective response 2 h post-capture, but there was no indication that catch-and-release stimulated a shift in metabolism or acid-base regulation.

5. Recommended best practices

Across all fishing sectors and locations along the migration pathway, levels of RM in Pacific salmon can be linked to gear types, gear use, capture and handling practices, and environmental conditions. Based on the scientific evidence reviewed above and the scale of RM outlined in Table 1, herein we generate a series of best practice recommendations which aim to enhance survival of captured and released Pacific salmon by minimizing physical injury and physiological impairment (Table 2). Most of these recommendations are focused on practices that can be adopted in Pacific salmon directed fisheries because it may be less feasible for non-Pacific salmon directed fisheries to modify their practices accordingly. Several recommendations are likely also applicable to other fish species fisheries that are captured as bycatch or targeted in catch and release fisheries. Fisheries should use gear and adopt approaches that minimizes injury, stress, and reduces bycatch, whereby certain best practices carry more weight depending on the stage of the Pacific salmon's homing migration, and others require identifying trade-offs. Our hope is that these recommendations will be embraced by fishers, fishing communities, and fisheries managers, incorporated into fishing regulations, and used as guidelines to enhance survival of released fish. We acknowledge that depending on the context of an individual fishery, RM may or may not be relevant to achieving sustainable fisheries at the population level (Corsi et al. In Press.a) but individual outcomes are still relevant to fish welfare and providing fishers an opportunity to engage in responsible behaviours (Cooke et al. In Press.b).

Our risk analysis (Table 1) showed that in terms of fishing gear type, purse seines and gill nets yielded proportionally more "very high risk" RM outcomes (4/5 and 8/11 studies, respectively) than the other gear (e.g., 5/12 angling studies, and 2/8 beach seine studies). The primary issue with purse seines is that bycatch often remains in nets and on board too long resulting in injury and asphyxiation leading to poor survival after release. Gill nets also cause similar outcomes for bycatch resulting from long periods of time when fish are entangled. Gill nets maybe the riskiest gear because, unlike purse seines, they are used in all three environment types and over a large range of soak times, including warm rivers where gear interactions can lead to extremely high RM, whereas purse seines are primarily used in cooler marine environments.

Mortality risk associated with purse seine fisheries can be mitigated

by using a brailer to sort a subset of the catch while the remaining fish are held in deep oxygenated water during sorting (Cook et al., 2019b). Using a brailer, rather than 'stern hauling the net' reduces on deck handling time and crushing injuries, and therefore hypoxia, exhaustion and injury. For larger sets, crowding induced injury and hypoxia can be reduced by keeping the net loose during holding in the brailer (i.e., reduce net constriction; Cook et al., 2018b). Purse seine fisheries should also release non-target fish as soon as possible, as periods longer than 5 mins result in increased mortality risk (Cook et al., 2018b). Decreased holding periods may be facilitated by reducing set sizes and prioritizing the release of bycatch. In sets where there is high incidence of bycatch, fishers could avoid landing bycatch by releasing them directly into the water using the brailer (Grande et al., 2019). Alternatively, wet chutes can serve as a means of releasing landed fish overboard quickly with little injury (as in tuna purse seine vessels; ICCAT, 2008; Cook et al., 2018b). Targeting smaller set sizes will also limit the risk of injury caused by extended confinement and crowding period, such as fish rubbing against the brailer and running into one another (Cook et al., 2018b). However, smaller set sizes would result in lower catch per unit effort (CPUE). Likewise, injury could be mitigated by selecting a mesh size that reduces injury or capture of non-target species and sizes, but this can be challenging because fish are highly variable in size and fishers need to balance the trade-off between catch rates and drag. Other mitigation measures include sorting fish in shade and spraying water onto sorting tables, chutes, and the deck to reduce thermal stress and transporting fish between handling decks using a conveyor belt or chute to reduce handling time and hypoxia.

Two of the most direct measures to minimize bycatch mortality for gill nets is by reducing soak time – either by removing nets earlier or checking them more frequently – and selecting a mesh size that best matches the target species size but avoids gilling bycatch (Cook et al., 2019b). However, as in purse seine fisheries, reducing soak time also reduces CPUE, rendering this mitigation measure less practical for harvesters. Likewise, identifying a mesh size selective toward a target species is challenging given that even a slight variability in size of bycatch species can be the difference between a fish becoming tangled versus gilled. Injury and asphyxiation can also be mitigated by deploying a stiff, tight net that reduces entanglement severity (Cook et al., 2018b; Reid, 2020). Entangled bycatch should be detangled rapidly, underwater, limiting air exposure duration within 10 s, and by cutting the net (Cook et al., 2015). Although a cut net would require further effort to be repaired, forcing fish through the mesh increases handling time and injury, heightening the risk of RM.

Notably, Pacific salmon are more resilient to injury once they reach terminal spawning areas, such that gill nets have been shown to produce injuries that were indistinguishable from beach seines (Bass et al., 2018b). These findings suggest that RM could potentially be reduced by using beach seines instead of gill nets in estuarine and lower river environments, until migrants have reached a point in their migration/maturation where they have greater resilience to capture and where thermal refugia for physiological recovery may be more available.

As in purse seine fisheries, beach seine fisheries should ensure sufficient water is in the net during sorting to maintain oxygen levels (Raby et al., 2012a, 2014a). Set sizes should be kept small to allow quick sorting, particularly if water levels are shallow or temperatures are high (i.e. >18°C), and nets should be kept loose during sorting to minimize crowding injuries and stress. Often the net is pulled farther up shore to facilitate sorting, but this leaves little water in the net, increasing risk of asphyxiation. Beach seines should not be pulled too shallow if the set is large or there is low water velocity flowing through the net. We also suggest prioritizing the release of bycatch, which can be especially difficult if sorting in deep water and if the release species is more likely to dive.

Hook and line-based Pacific salmon directed fisheries should avoid treble hooks or tandem hooks and instead use single barbless hooks or

circle hooks (but only if fishing passively) to reduce risk of foul- or deep-hooking (e.g., hooking the eye through the mouth cavity or gut; Grover et al., 2002; Hinch et al., 2024). For troll fisheries, reducing trolling time is also recommended to mitigate exhaustive exercise and injury. However, adopting barbless hooks and limiting soak time can also decrease CPUE and capture success, which could be problematic for commercial fishers. Other mitigation measures include limiting fight time by using heavy tackle and reeling fish in as quickly as possible to reduce metabolic recovery duration, and therefore reducing the risk of post-release predation or behaviour alterations (e.g., forgoing feeding or mating; Birnie-Gauvin et al., 2023; Hinch et al., 2024). Handling bycatch should be minimized whenever possible to reduce handling-related injuries, such as fin damage and scale loss, and physiological stress from hypoxia (Cook et al., 2015; Hinch et al., 2024). We suggest fish be released at the water-line whenever possible and dehooked using pliers, a gaff, or cutting the line if fish are deep-hooked. If fishing from a boat, detangling, handling (if necessary) and species identification should be conducted in water. The use of a boat-side sling can facilitate this (Hinch et al., 2024). In cases where bringing fish out of the water is necessary, air exposure should be kept < 30 s, particularly in estuarine and lower river environments where thermal and osmoregulatory pressures delay recovery of released fish (Cook et al., 2015; Hinch et al., 2024; Lunzmann-Cooke et al., 2024). The use of handling nets, even ones believed to be ‘fish friendly’, should be avoided if there is a possibility that fish will be released, particularly in marine and estuarine environments, as Pacific salmon are prone to scale loss and fin damage upon interaction with nets. Fish should only be handled with bare wet hands on the belly and caudal peduncle to minimize removing mucus and scales (if not yet reabsorbed) (Keefe et al., 2022; Hinch et al., 2024).

For all gear types, if bycatch encounters are high, or there is a high likelihood that fish will not be retained, we advise fishers move locations or change to a gear that is more selective to the target species (e.g., swapping to a larger mesh size or changing hook size). This will happen most frequently for non-Pacific salmon directed fisheries and when this occurs, management may adopt a reactive approach and close the fishery. In 2024, the Kodiak Alaska trawl fishery for lucrative Alaska pollock was closed weeks early after 2000 Chinook salmon, potentially bound for BC, were captured as by-catch (Herz, 2024). Because of the size and mass of trawl nets, RM may be 100 % for by-catch. Given the low abundances of BC Chinook salmon, and the economic importance of the pollock fishery, we need to be rethinking the approach of these types of fisheries to better protect Pacific salmon and still maintain a viable targeted fishery (Campbell, 2025).

Regardless of gear selection, warm water temperatures threaten Pacific salmon post-release survival by causing physiological stress and promoting pathogen virulence. Closing fishing times in Pacific salmon directed fisheries in response to high water temperatures is a widely recommended management strategy (Van Leeuwen et al., 2021; Birnie-Gauvin et al., 2023). Recent studies have also shown that the impact of temperature is reduced when thermal refuges are available as fish will seek cool water upon release; a behaviour that has been attributed to energy conservation and heightened reproductive success (Minke-Martin et al., 2018; Elmer et al., 2022). Fishing activities should therefore aim to be conducted when water temperatures are the coolest, such as morning, rather than late afternoon, and target locations next to thermal refugia (e.g., near a cool water tributary). Thermal refugia are available in marine fisheries, where Pacific salmon can swim to deep water upon release, and also in freshwater fisheries where there are lakes. Fishing in the estuarine environment poses the highest risk for RM as Pacific salmon are contending with physiological transformations and pathogenetic shifts as they transition from saltwater to fresh water (Teffer et al., 2018; Bass et al., 2019), and there are limited thermal refuge opportunities without major salinity gradients that cause further stress. Evidence also indicates there are carry-over effects from marine and estuarine fisheries that affect fish survival in fresh water. For example, Chinook salmon did not survive their homing migration in

fresh water > 20°C if they had previously been captured in a cool marine environment but air exposed for longer than 30 s (Hinch et al., 2024). Therefore, as water temperatures continue to warm with climate change, it may be worth considering focusing fishing in marine or terminal areas where thermal refugia exist, and limiting fishing activities in estuaries and early freshwater entry. A further advantage of focussing fisheries in terminal areas is that it reduces the likelihood of bycatch (e.g., non-targeted stock or species, sublegal fish).

5.1. Facilitated recovery

Facilitated recovery approaches are widely used tactics endorsed by fisheries groups and agencies (e.g., DFO, 2023d) intended to improve post-release survival of captured fish in Pacific salmon directed fisheries. Recovery methods have been used in commercial fisheries involving on board troughs (e.g., Fraser Box) which utilize high speed water to ‘ram ventilate’ fish (Farrell et al., 2001; Buchanan et al., 2002). In recreational fisheries, flow through, soft mesh bags are sometimes used to place fish into, with anglers orienting bags into the prevailing flow. More often, fish are held by anglers and moved in a ‘back-and-forth rocking’ technique in an attempt to increase water flow over the gills (Donaldson et al., 2011a; Brownscombe et al., 2013; Donaldson et al., 2013; Robinson et al., 2015). Fish respiration relies on an oxygen gradient between water and gills when water flows through the mouth and out the opercula (Gilmour, 1997). Hence, moving fish back and forth is not efficient at promoting oxygen transfer (Pelletier et al., 2007). The efficacy of facilitated recovery tactics is case-dependent. Whereas some studies have observed immediate benefits such as improvements to impaired equilibrium, benefits to longer term survival or spawning success generally have not been realized (Donaldson et al., 2013 [pink salmon]; Nguyen et al., 2014 [sockeye salmon]; Raby et al., 2014 [coho salmon]).

Facilitated recovery approaches will only reduce RM and generate long-term benefits if the main physiological issue associated with capture/handling event is anoxia and disequilibrium brought on by excessive anaerobiosis and in particular associated with warm water capture and/or prolonged air exposure. Most captured fish are injured which by itself cannot be helped by facilitated recovery approaches. The confinement of bags or the physical restraint of holding fish during any recovery attempt increases physiological stress (e.g., heightened cortisol, lactate, and hematocrit levels; Farrell et al., 2001; Donaldson et al., 2011; Robinson et al., 2013) and could further injure fish by removing scales and mucous, damaging fins, and increasing air exposure. Given the limited evidence for increases in survival with device-based, or hand-facilitated, recovery approaches in Pacific salmon fisheries (except see Farrell et al., 2001), and the likelihood of reduced survival, the best recovery approach may be to release fish immediately thus reducing handling, air exposure, and further injury. The exception may be if fish are so highly impaired that they cannot maintain equilibrium thus they have limited ability to avoid predators, so a brief recovery period may be necessary. Because recovery is aided by highly oxygenated water, fishes’ ability to rapidly access this if available at depth is another reason why minimal recovery and rapid release is needed in marine or lake fisheries.

5.2. Future directions

Across all fisheries, the role of fishing effort on RM has received little attention, with evidence indicating increased catches per set and capture and handling durations can cause considerable sublethal effects. For instance, a study in a tributary of the Fraser River found that although sockeye salmon were more likely to be injured when escaping from gill nets in the lower Fraser River when fishing effort was high, there was no evidence that fishing effort was related to injury severity (Kanigan et al., 2019). It is possible that fish with severe injuries died upon escape before reaching the tributary which could bias the apparent effects of

Table 2

Recommended best practices to reduce major release mortality (RM) concerns in relation to Pacific salmon fishery type, activity, and location. Recommendations were either stated in the cited sources and/or are based on our interpretation of their findings in the context of the reviewed literature.

Fishery type	Fishery activity	Fishery Location	RM concern	Recommendation	Source
All fisheries	Gear Deployment	All locations	Temperature stress	Avoid fishing when water temperatures exceed 18°C - 19°C	Eliason et al. (2011); Hinch et al. (2012), (2024); Gale et al. (2013); Bass et al. (2018a); Teffer et al. (2019), (2021); Reid (2020); Elmer et al. (2022)
Beach seine Gill net Angling	Fish Handling	All locations	Hypoxia Reflex impairment	If air exposure is necessary, keep it < 30 s.	Cook et al. (2015), (2018b); Hinch et al. (2024)
	Fish Handling	Estuary	Hypoxia	Minimize capture duration and handling time (i.e., rapid release).	Farrell et al. (2001); Donaldson et al. (2011b), (2013); Raby et al. (2015a,b); Teffer et al. (2017)
	Fish Handling	Lower and upper river	Reflex impairment External and internal injury	Only attempt recovery methods if fish appear moribund (i.e., low RAMP score). Ensure cool moving water in recovery apparatus to maintain oxygen levels. Recovery approaches will not rectify bleeding or other injury issues.	
		Lower and upper river Terminal lakes and streams Marine Estuary Lower river	External injury Mortality of small bodied fish	When possible, fish close to spawning regions which ensures Pacific salmon have reached a level of maturity where they have greater resilience to wounding and scale loss, and this also minimizes concerns of harvesting mixed-stocks. Use larger net mesh sizes or smaller hook sizes to facilitate net escape, and reduce injury to undersized individuals.	Raby et al. (2013); Bass et al. (2018b) Cook et al. (2019b); Hinch et al. (2024)
All net fisheries	Gear Deployment	All locations	Minimize interaction with non-target Pacific salmon species Hypoxia External injury	Modify mesh size, deployment depths, and fishing locations to avoid non-target species. During sorting, prioritise releasing by-catch first.	Cook et al. (2019b) Raby et al. (2014a); Cook et al. (2019b)
Purse seine	Fish Handling	Marine Estuary Lower river	Hypoxia Reflex impairment External injury	Keep nets loose during fish boarding to reduce crowding and fish contact with vessel. Use brailing instead of ramp haul to board fish. On-board sorting should be on purpose-built tables rather than deck. Tables should be physically connected to a purpose built 'chute' to rapidly send bycatch overboard. Minimize hand grabbing of fish during sorting process. Minimize fish 'time on board' which should not > 5 min for fish to be released.	Cook et al. (2018b), (2019b)
			Thermal stress Hypoxia	Provide shade and water spray to sorting tables and chute so that an individual fish is not fully air exposed for more than 30 sec.	Cook et al. (2019b)
Beach seine	Gear Deployment	Estuary Lower river	External injury	Reduce length of nets which reduces large catch densities enabling quicker landing and less contact between fish and substrate.	Raby et al. (2014a)
	Fish Handling	Estuary Lower river	Hypoxia Reflex impairment	Keep net deeper during sorting to reduce crowding enabling higher oxygen levels.	Raby et al. (2012b), (2014a)
Gill net	Gear Deployment	All locations	High levels of net escape and poor spawning success of escaped fish.	Transition away from using gill nets entirely Less injurious alternatives are readily available (e.g., in estuarine environments – trolling, in freshwater environments - beach seines, weirs and trap boxes.)	Baker and Schindler, (2009); Bass et al. (2018a); Kanigan et al. (2019)
			Reduce high capture rates of by-catch External injury	Alter depths of nets to minimize bycatch interception. Use larger mesh sizes, increased tautness and multifilament nets to reduce wounding. Minimize gillnet use during times when encountered fish are less mature - more mature fish have greater resilience to net injury.	Freshwater et al. (2024) Raby et al. (2013); Bass et al. (2018b); Cook et al. (2019b); Reid (2020)
	Fish Handling	All locations	Hypoxia Reflex impairment External injury	Use short soak times checking nets frequently so that by-catch can be released as soon as fish are captured. Remove by-catch from net quickly and when possible, under-water. Cut net to release entangled fish if necessary.	Bass et al. (2018a); Cook et al. (2019b); Reid (2020) Teffer et al. (2017); Cook et al. (2019b)
All hook and line fisheries	Gear Deployment	All locations	External and internal injury	Use single hooks with a maximum gap width of 15 mm.	Cook et al. (2019b); Lunzmann-Cooke et al. (2023); Hinch et al. (2024)
Angling	Gear Deployment	Marine Estuary Lower river	External and internal injury Reduce by-catch encounter rates.	Use artificial lures/bait to reduce the risk of deep hooking compared to live bait. Move locations or alter gear (e.g., increase size of net mesh [for net-based fisheries] or lure size [for hook-based fisheries]) to limit interactions with undersized fish or non target species.	Cook et al. (2019b) Lizée et al., 2018; Hinch et al. (2024)
			Depredation	Avoid fishing in locations with high predator occurrences.	Hinch et al. (2024)

(continued on next page)

Table 2 (continued)

Fishery type	Fishery activity	Fishery Location	RM concern	Recommendation	Source
			External and internal injury	Use single barbless circle hooks instead of treble hooks or “J” hooks, and hooks with a 15 mm maximum gap width (e.g., “Octopus” style hooks 1.3 mm diameter and 31 mm length). Avoid tandem hooking arrangements with hoochies and bait.	Cook et al. (2015), (2019b); Hinch et al. (2024)
	Fish Handling	All locations	External and internal injury	Avoid using landing nets, even those considered fish friendly, instead release fish at water line using purpose-built tools. If fish must be landed, use rubber-coated, knotless net with thick webbing and very small mesh size. Cut line when fish are deeply hooked. Only handle fish with bare wet hands, and limit areas of contact to caudal peduncle and under the pectoral fins. Avoid holding fish vertically by only the tail or touching vital organs (e.g., gills).	Cooke and Danylchuk, (2020); Lunzmann-Cooke et al. (2023); Hinch et al. (2024)
			Hypoxia Reflex impairment	Use lines with break strength that will not extend fight durations.	Cook et al. (2015)

fishing effort. Increased gill net fishing effort may produce longer entanglement periods, which increases the risk of hypoxia (from either asphyxiation or exhaustive exercise), injury, and depredation, ultimately resulting in higher RM (Buchanan et al., 2002; Uhlmann and Broadhurst, 2015). It is also possible that seine or gill net fishers may increase their CPUE either by broadening the area covered by a seine tow or extending gill net soak times, which will increase the risk of hypoxia, reflex impairment, and injury to by-catch when on-board sorting begins (Raby et al., 2012a, 2014a; Cook et al., 2019b). Given the growing evidence relating fishing effort to fish impairment and injury, more research is required to better incorporate fishing effort into estimates of RM and management decisions to limit RM.

Although most Pacific salmon directed fisheries target maturing homing salmon, smaller fish are also frequently caught and released if they fall below legal-size limits, particularly with Chinook salmon, or in the hopes of catching a larger fish in recreational fisheries. However, across many gears and fisheries, smaller or sub-legal sized Pacific salmon are more prone to injury and more likely to suffer high RM (Washington Department of Fisheries, 1993; Baker et al., 2011; Bass et al., 2018b; Kanigan et al., 2019; Hinch et al., 2024; Lunzmann-Cooke et al., 2024). Complicating the matter further, most studies examining RM have focused on legal sized (e.g., larger) individuals, potentially biasing estimates of RM, which are likely too conservative when assessed at the population level (Table 1; Hinch et al., 2024).

Identifying best practices that should be integrated into policy poses a significant management challenge as policies can affect fishers differently depending on their motivations for fishing. For instance, gear with lower retention/catchability rates are inherently going to have lower risk of RM but are less favourable for retention fisheries. Furthermore, although most best practice recommendations are straight forward for reducing individual RM risk (e.g., do not fish in rivers with high water temperatures), others require evaluating trade-offs and selecting the approach with the least risk to the desired outcome. For example, de-hooking a fish without landing gear (i.e., a net) can be challenging, particularly for inexperienced anglers, in which case, using landing gear might be lower risk because it will decrease the time fish spend being angled and handled. Most research examining RM on Pacific salmon focused on the individual-level, yet it cannot be assumed that any effort to maximize individual RM also reduces mortality at the population level (Corsi et al., In Press.a). In fact, in some cases, modifying fishing regulations to reduce individual RM may actually increase population level mortality. For example, fishing during colder seasons may increase catchability (Van Leeuwen et al., 2021; Keefe et al., 2022), potentially resulting in higher population-level mortality, despite having lower individual RM rates compared to fishing in warmer periods. Similarly, given that Pacific salmon fisheries are often mixed stock fisheries, particularly in the marine environment, mortality may be

higher at the population level when release is allowed even with decreased individual RM rates compared to if fisheries retained all catch. Ensuring that the scale of research is communicated and that population-level management outcomes are considered when modifying fisheries management regulations is therefore important to ensure efforts are contributing to the desired outcome (Corsi et al. In Pressb). Overall, integration of science into management is a cautious process (Young et al., 2013), and voluntary fisher compliance plays an important role in reducing RM. In some cases, education may be more effective than regulation. For example, aside from a few exceptions, air exposure regulations have rarely been implemented yet management agencies and other fisheries stewardship organizations routinely encourage that anglers minimize air exposure. Even when regulations are implemented, they should be accompanied by education and outreach efforts to improve compliance.

Eventually, technology (e.g., near real-time genetic sequencing) and analytics (e.g., high resolution spatio-temporal distribution models) may allow for dynamic ocean management to implement measures that limit fishing impacts on non-targeted fish (e.g., sublegal fish or more vulnerable stocks; Hazen et al. (2018)). However, until such methods are developed and refined for Pacific salmon fisheries, simpler fisher behaviour modifications remain necessary to reduce RM risk. One potential means to improve individual RM is to go “back to the future” and evaluate the use of more traditional fishing methods – such as beach seines (discussed herein), weirs, fish wheels, dip nets, and reef nets – which may involve less injurious ways of capturing and releasing fish (Atlas et al., 2017, 2021; Campbell, 2025). Such gears have been used for selective harvest by Indigenous groups for millennia with the use of weirs dating back > 3000 years (Moss et al., 1990). Different traditional fishing methods have been applied across the Pacific salmon migration spectrum, for instance reef nets were used in coastal environments, fish wheels and weirs were used in rivers, and dip nets were used near rapids and waterfalls further up-river (Atlas et al., 2021). Traditional fishing methods have generally been excluded from RM evaluations given the lack of studies examining their associated risks compared to other gears, such as selectivity (i.e., risk of bycatch) or injury frequency and severity. The potential benefits of traditional fishing gear to reduce individual RM and help with the sustainability of the Pacific salmon fisheries highlights the need to further research their associated risk.

6. Conclusions

Fishers release Pacific salmon from all gear types for a variety of reasons including regulations, high grading, conservation goals, and ethical concerns. However, the benefits of releasing captured fish depend on whether they survive and are not impaired in terms of their ability to subsequently spawn. This review summarises research

examining risks, levels and mechanisms of RM for Pacific salmon and recommends actionable best practices to promote survival. We show that certain gear, fishing approaches and environments have less risk of RM than others (e.g., beach seine and angling can be done with lower RM risk than gill nets and purse seines), locales with thermal refuges (e.g., coastal zones, lakes) will have lower RM than areas of physiological transition (e.g., estuaries, lower rivers). We have suggested means to modify fishing practices to reduce RM across all fishing sectors, yet while many of our recommendations can be regulated via policy or management actions (e.g., soak time, hook size, temperature cut-offs), some will depend on fishers voluntarily modifying their behaviours (e.g., minimizing air exposure, not fishing if predators are nearby). Fisher motivations and beliefs, and management restrictions (e.g., for recreational fishing, voluntary catch and release- vs. regulation-motivated) are important to consider given some measures may be less effective or not applicable depending on fisher behaviour (e.g., anglers stopping fishing once quota is captured would not apply to an angler practicing voluntary catch-and-release). However, fishers are generally receptive to applying new conservation measures if there is evidence showing recommendations reduce RM (Raby et al., 2014a; Hinch et al., 2024; Watson et al., 2018). Methods to estimate and study RM have improved considerably over the past two decades with the advent of more sophisticated telemetry tags and receiver networks, and the realization that RM is a process that starts the moment a fish encounters fishing gear and its effects continue to be seen weeks later. Therefore, there is a need to increase awareness of this phenomenon to gain support and encourage implementation of best practices. RM is likely the largest component of FRIM, but there are other mortality agents not included in current mortality estimates because the magnitude of their impact is unknown (e.g., depredation; Patterson et al., 2017a, 2017b). Despite this, there is little doubt that across all sectors and each phase of the Pacific salmon migration trajectory: i) fisheries interactions impose physical and physiological stress that can negatively affect fate of released fish, ii) mechanisms underpinning fisheries-related mortality evolve as Pacific salmon migrate and mature, and, iii) consequences of fisheries interactions are heightened by warming temperatures, a trend that is expected to worsen with climate change. Adopting best practices to reduce stress and injury severity is crucial if we are to continue relying on releasing fish from capture as a management and conservation strategy.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Scott G. Hinch reports financial support was provided by British Columbia Salmon Restoration and Innovation Fund. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Funding was provided by the British Columbia Salmon Restoration and Innovation Fund. We thank E. Eliason, A. Bass, and D. Moulton for their helpful discussions on the paper concepts and figures.

Data availability

No data was used for the research described in the article.

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