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Anaerobic Exercise and Recovery: Roles and Implications for Mortality in Pacific Salmon

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ABSTRACT
Routinely, fish encounter stressors and conditions that require the use of anaerobic exercise, including escaping predators, capturing prey, and interacting with fisheries. Although anaerobic metabolism rapidly yields energy to support locomotion, it also accelerates the depletion of energy stores, and accumulates potentially damaging metabolites, relative to aerobic metabolism. During recovery from intense exercise, animals are vulnerable and may forgo opportunities (e.g., foraging, mating). Recovery is thus likely under strong selection pressure. Despite the fact that recovery is essential for life, relatively little attention has been given to its importance for fitness and survival. Here, the ecology and physiology of recovery following intense exercise are reviewed using Pacific salmon (*Oncorhynchus* spp.) as a model, though findings are relevant to a wide range of species given that the need for recovery is ubiquitous. Specifically, when and why salmon use anaerobic exercise across their lifecycle, the physiological consequences of this extreme exercise, and the recovery process are considered. The importance of considering recovery for effective management and conservation of Pacific salmon species is discussed, and examples to highlight meaningful ways in which knowledge of recovery can be applied to problems facing fish are provided, with implications widely applicable to all fishes. Given current and projected climate scenarios, understanding the role of temperature in recovery will become progressively more important, and should be an explicit consideration when assessing vulnerability.

KEYWORDS
Aerobic scope; anaerobic metabolism; conservation; excess post-exercise oxygen consumption (EPOC); exhaustive exercise; lifetime fitness; metabolites; respirometry; stress

1. Introduction

Fish encounter a gamut of challenges and conditions that require them to perform anaerobic burst exercise, such as chase prey, escape predators and fishing gear, or migrate through adverse hydraulic conditions. This form of metabolism mobilizes energy quickly to be readily utilized for powering muscles (Blažka 1958) but results in a variety of downstream physiological impacts that can range from mild to severe, depending on the type and duration of anaerobic exercise (Kieffer 2010). Small bursts of anaerobic exercise may be remediated rapidly, but intense exhaustive anaerobic exercise can be hugely detrimental (Black 1958; Wood et al. 1983; Holder et al. 2022). As such, timely *recovery* from intensive anaerobic exercise is necessary for fish to resume routine activities. Because recovery from exhaustive exercise is an essential part of life, it is likely under strong selection pressure since fish are vulnerable (e.g., to predation, fisheries) and miss opportunities to enhance fitness (e.g., *via* foraging, finding mates, competing for territory, continuing migration) when recovering.

Here, the ecology and physiology of recovery from anaerobic exercise in Pacific salmon (*Oncorhynchus* spp.) are reviewed. Pacific salmon comprise six species: sockeye salmon (*O. nerka*), Chinook salmon (*O. tshawytscha*), pink salmon (*O. gorbuscha*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), and steelhead/rainbow trout (*O. mykiss*). Pacific salmon are a good genus to review given the availability of data on anaerobic exercise and recovery, as well as a highly relevant group given their declining status across their range, and their cultural, ecological, and economic importance across the Pacific Northwest of North

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America and Eastern Asia. Pacific salmonids are rooted in the center of social–ecological systems that have supported Indigenous peoples for millennia, through practices involving, for example, cultural and spiritual beliefs (Atlas et al. 2021). From an ecological perspective, it is well known that brown bears (*Ursus arctos*) rely heavily on Pacific salmon as a source of fat and protein prior to hibernation, and their activity level has been linked directly to Pacific salmon spawning phenology, highlighting the role that these salmonids play within the broader ecosystem (Deacy et al. 2019). Economically, Pacific salmonids are also very profitable; the sockeye salmon fishery in Bristol Bay (Alaska) alone created $1.5 billion US dollars in revenue across the United States in 2010 (Knapp et al. 2013). Despite their importance however, wild Pacific salmon numbers are dwindling for many southern latitude populations (Governor's Salmon Recovery Office 2020; COSEWIC 2020a, 2020b). The upstream migrating adult life stage seems to be particularly vulnerable to increased river temperatures and abundant interactions with fisheries, but the mechanisms driving population declines are diverse (Ruckelshaus et al. 2002; Patterson et al. 2017a; Hinch et al. 2021), and not fully understood.

Hatched in freshwater habitats ranging from Japan, to Russia, to Alaska, and to Southern California, wild Pacific salmonids have piqued the curiosity of scientists for centuries. Once they hatch from their eggs, alevins rely on a yolk sack as a source of energy, until they emerge from the gravel to reach the fry stage and begin to actively forage (Groot and Margolis 1991). In some species, fry will begin feeding in natal streams and rivers, while others will migrate to lakes or even estuaries to begin exogenous feeding (Groot and Margolis 1991). At the parr stage (between 6 months to 2 years after hatching depending on location), these salmonids will continue to feed, and begin to transition into the smolt stage before migrating to sea. These early freshwater stages and the smolt migration are considered challenging as predation risk can be elevated (Collis et al. 2002; Osterback et al. 2013; Furey et al. 2016). Once at sea, smolts have access to abundant food sources, and undergo the bulk of their somatic growth (Groot and Margolis 1991). Adults return in large numbers from the ocean after several years of feeding and many undergo impressive, energetically demanding upriver spawning migrations (Hinch et al. 1996). Long and difficult migrations on the west coast of North America have selected for semelparity; with the exception of steelhead trout (*O. mykiss* Walbaum 1792), Pacific salmon have a single opportunity to spawn (Groot and Margolis 1991). Somatic energy conservation therefore plays a central role in successful upstream migration given that Pacific salmon cease feeding upon freshwater entry (Brett 1995; Crossin and Hinch 2005). Adults rely on endogenous energy stores to fuel migration, reproductive maturation, competitive behavior and the final spawning event. For this reason, energy-conserving traits are under strong selection, including cardiac and aerobic performance, morphologies and behaviors. For example, populations that undergo longer, more challenging migrations are more fusiform in shape (Hinch and Rand 2000; Crossin et al. 2004), have higher absolute aerobic scope (Eliason et al. 2011), lower reproductive investment (Kinnison et al. 2001; Crossin et al. 2004), and are genetically different (Hecht et al. 2015) than those with shorter, easier migrations.

Pacific salmon have evolved to be experts at both aerobic and anaerobic swimming in order to minimize metabolic costs and maximize performance (Brett 1995; Eliason et al. 2011; Eliason and Farrell 2016). During aerobic swimming, oxygen fuels locomotion *via* oxidative phosphorylation to produce large amounts of adenosine triphosphate (ATP, an energy "currency"). As such, this form of swimming is used for indefinite periods of time (sustained swimming), including during migration, or to maintain position in currents, and relies primarily on oxidative red muscle fibers. In contrast, anaerobic swimming does not require oxygen to fuel locomotion, and instead relies on the breakdown of glycogen to rapidly produce significantly less ATP *via* anaerobic glycolysis (Black et al. 1966). Anaerobic metabolism is triggered when faced with hypoxic or anoxic conditions, but also during intense exercise, when oxygen demand is maximal and most limited, to fuel powerful muscle contractions *via* glycolytic white muscle fibers, and thus enhance swimming capacity (i.e., faster, more powerful swimming) (Beamish 1978). An oxygen debt is incurred from anaerobic swimming (i.e., termed EPOC: excess post-exercise oxygen consumption), and oxygen must be replenished to reestablish homeostasis (e.g., restore oxygen stores, phosphates, glycogen, ionic balance; Milligan 1996; Lee et al. 2003). This oxygen debt is assumed to be the cost of returning to a resting state; that is, the cost of fueling metabolism with the products of anaerobic metabolism, resynthesizing pre-exercise fuel stores, and restoring hormone, ionic and osmotic imbalances, and is estimated by measuring aerobic metabolism during recovery (Wood 1991; Nelson 2016).

There is increasing evidence that Pacific salmon are periodically unable to recover from anaerobic metabolism following intense challenges (e.g., high flows and dynamic river conditions, high temperatures, fisheries interactions; Gale et al. 2011; Eliason et al. 2013a; Burnett et al. 2014a, 2014b; Kraskura et al. 2020), so the objective of this review is to answer the following questions: 1) What are the physiological and behavioral consequences of anaerobic exercise?, 2) When and why do Pacific salmon use anaerobic exercise?, 3) What happens during recovery?, 4) What can be done to facilitate recovery?, and 5) What are the most pressing knowledge gaps that must be addressed? Given that many Pacific salmon are currently threatened or endangered (NOAA 2016; Governor's Salmon Recovery Office 2020; COSEWIC 2020a, 2020b), there is a need to determine the physiological limits of salmon, and further understand when and why salmon are pushed beyond these limits. While there are likely many causes for increased Pacific salmon mortality, this review focuses on how anaerobic exercise and recovery contribute to this mortality. Although this synthesis is focused on Pacific salmon, the findings discussed here are applicable broadly across a wide range of fishes given that the need for recovery following intense anaerobic exercise is ubiquitous.

2. What are the physiological consequences of anaerobic exercise?

High intensity exercise requires energy, so it can result in the depletion of three primary endogenous fuels: ATP, phosphocreatine (PCr), and glycogen (Milligan 1996). In the first stage of exhaustive exercise, fish use the energy derived by the hydrolysis of PCr, so PCr levels immediately decline in muscles, though to various extents (40–90%; Dobson and Hochachka 1987; Schulte et al. 1992; Wang et al. 1994). Concomitantly, ATP levels in the muscles also decline, again to variable extents (24–90%; Dobson and Hochachka 1987; Schulte et al. 1992; Milligan 1996). PCr and ATP reductions lead to the activation of glycogenolysis, thereby depleting glycogen stores in the white muscle by up to 90% (Dobson and Hochachka 1987; Milligan 1996). This has been extensively studied under laboratory conditions, but less so in the wild. Pon et al. (2012) explored how fish passage affected the physiology of pink salmon using muscle biopsies, and demonstrated that muscle glycogen and PCr declined following the ascent of the fishway, supporting the idea that such exercise recruits anaerobic pathways. Eliason et al. (2020) showed similar findings in sockeye salmon exposed to a mild capture event (beach seine). The depletion of primary endogenous sources of energy in the skeletal muscle thus also contribute to muscle fatigue.

A rapid and short-lived increase in catecholamines (adrenaline and noradrenaline), as well as a steep increase in plasma cortisol levels also occur following intense exercise (Milligan 1996). Elevated catecholamines increase heart rate (f_H) and energy mobilization, so both an increase in f_H and glucose are expected early during exercise (Stevens and Randall 1967; Romero and Wingfield 2001; Clark et al. 2010). Cortisol, the primary stress hormone in fish, can increase 5-fold and remain elevated for over 6 hr post-exercise (Milligan 1996). Here, high cortisol concentrations appear to inhibit glycogenesis given that glycogen synthesis in the muscle does not begin until cortisol levels have declined (Pagnotta et al. 1994). Nonetheless, it is well known that increased cortisol is a component of the stress axis, inducing the mobilization of energy reserves, and diverting resources away from non-vital processes such as reproduction (Mommsen et al. 1999; Fullerton et al. 2000). This response is protective and adaptive in the short-term as energy is diverted to maximize survival, but is disadvantageous over prolonged periods as it compromises reproductive output, immunity, swimming capacity and overall survival (Romero and Wingfield 2001).

Exhaustive exercise results in severe metabolic, acid-base, osmotic, and endocrine disturbances, which in some cases can be severe enough to cause death (Wood et al. 1983; Milligan 1996; Eliason et al. 2013a, 2013b). In the presence of oxygen, carbohydrates, proteins, and lipids are oxidized *via* the citric acid cycle (Kreb's cycle) and the electron transport chain to produce large quantities of energy (~36 ATP) (Kieffer et al. 1998; Richards et al. 2002). In the absence of oxygen, carbohydrates—glycogen in particular—are converted to pyruvate through glycolysis producing comparatively less energy (2 ATP; Black et al. 1966). This also occurs in the presence of oxygen, but during anaerobic metabolism, pyruvate is quickly broken down to lactate *via* lactate dehydrogenase (LDH) instead of continuing on to the citric acid cycle. The production of lactate, concurrent increase in partial pressure of CO_2 (P_{CO2}), and substantial release of protons (H^+) into the blood by white muscles, are associated with an increase in acidity, thus low blood pH (i.e., acidosis). Particularly during exhaustive exercise, this build-up of lactate can become noticeable within minutes, and has been associated with death in many Pacific salmon species (Black 1957a, 1957b; 1958; Wood et al. 1983; Cooke et al. 2006, 2008; Young et al. 2006; Crossin et al.

2009; Pon et al. 2009a, 2009b; Jeffries et al. 2012). The consequences of acid-base and osmotic disturbances can be severe, including an increase in hematocrit and plasma protein, a decline in hemoglobin binding affinity, diminished contractility of cardiac muscles, ionic imbalances (increased plasma potassium, [K^+], sodium, [Na^+], and chloride, [Cl^-]), and even cellular damage (Wood and Randall 1973a, 1973b; Wood et al. 1983, Wood 1991; Hanson et al. 2006). Both osmotic and acid-base imbalance are a major limiting factor for recovery in salmon, and are likely a proximate cause for mortality. Even once P_{CO2} returns to normal, acidosis persists and can further reduce the binding affinity of oxygen to hemoglobin, causing oxygen saturation to decline from 100% to 33–61% (Green and Root 1933; Black 1958). Salmonids do however have access to carbonic anhydrase in the plasma, which allows them to deliver oxygen to tissues even under acidosis (Harter et al. 2019), mitigating some of the consequences of acidosis, but these disturbances nonetheless require recovery.

The steep and extended increase in plasma [K^+] (i.e., hyperkaleamia) has major consequences on the physiology of fish. The increase can be as high as 2-fold resting values, and last for >12 hr (Wood et al. 1983). This increase in plasma [K^+] is primarily due to a release of K^+ from skeletal muscles (Holk and Lykkeboe 1998), but is exacerbated by acidosis and/or cellular damage, causing the release of intracellular contents. This ensues further cellular damage, modifies electrochemical gradients and affects locomotor and heart muscle function (Hanson et al. 2006; Moyes et al. 2006). For example, potassium loss from the skeletal muscles could decrease membrane excitability and compromise muscle contractions, contributing to muscle fatigue (Sjøgaard 1991; Bers 2000). The same is true for cardiac muscle, resulting in compromised cardiac output under hyperkalaemic conditions (Hanson et al. 2006).

Cardiac contractility is further reduced during exhaustive exercise by decreased oxygen diffusion to mitochondria in the working muscles, indicated by a decrease in venous partial pressure of oxygen (P_{VO2}). Low oxygen is a component of the so-called "triple threat" causing decreased contractility in the heart, along with low pH and high [K^+], but is less often considered perhaps due to its difficulty to measure *in situ* (Hanson et al. 2006; Eliason and Anttila 2017). Nonetheless, some studies have successfully measured venous oxygen levels such as Eliason et al. (2013a), who showed that P_{VO2} declined slightly between rest and steady swimming in sockeye salmon, but declined significantly further during bursting.

Finally, the physiological and biochemical impacts of exhaustive exercise appear to be sex- and life-stage specific. For example, upstream migrating, sexually mature females tend to have higher plasma lactate, glucose and cortisol than males (e.g., Schmidt and Idler 1962; Dick et al. 2018; Eliason et al. 2020). Plasma glucose, sodium and potassium responses to exercise differed depending on if fish were sampled early or late in the freshwater spawning migration (Dick et al. 2018).

3. When and why do Pacific salmon use anaerobic exercise?

In salmon, aerobic metabolism can support swim speeds of up to 70-85% of the critical swimming speed (Ucrit, a standard measure for assessing swimming capacity in fish) (Jones 1982; Burgetz et al. 1998; Beddow and McKinley 1999; Geist et al. 2003; Hvas et al. 2021a), after which salmon rely, at least in part, on anaerobic metabolism. This threshold is likely lower in less athletic fish species, for which aerobic metabolism likely supports swim speeds less than 70% of U_{crit}. Anaerobic metabolism generates ATP in the absence of oxygen, and does so much more quickly than aerobic metabolism to support more powerful swimming. Burst swimming relies on the recruitment of anaerobic white muscles (Brett 1964; Beamish 1978; Geist et al. 2003). Anaerobic metabolism is however less efficient than aerobic metabolism, producing 15–20 times less ATP (glycolysis produces 2 ATP while oxidative phosphorylation produces ~36–38 ATP per glucose molecule; Hochachka and Somero 2002), making it exceedingly costly. Despite this, the overwhelming majority of musculature in salmonids is white (anaerobic) muscle, indicating the importance of this resource to fish survival, serving as a type of "insurance policy"—it may not always be needed but without it, individuals would clearly be unable to survive to maturity and spawning.

There are several circumstances under which Pacific salmon use anaerobic exercise throughout their lifecycle (Figure 1), including during natural events (e.g., fry migration, foraging, escaping predators, ascending rapids and fast water, spawning migration, spawning), but also during encounters with anthropogenic challenges (e.g., fisheries interactions, human-made hydraulic and thermal challenges). Additionally, anaerobic demands can be modified or exacerbated by factors like water temperature, or hypoxia. The next section discusses when and why Pacific salmon use anaerobic exercise within each of these contexts, but begins with a discussion on how some biotic and

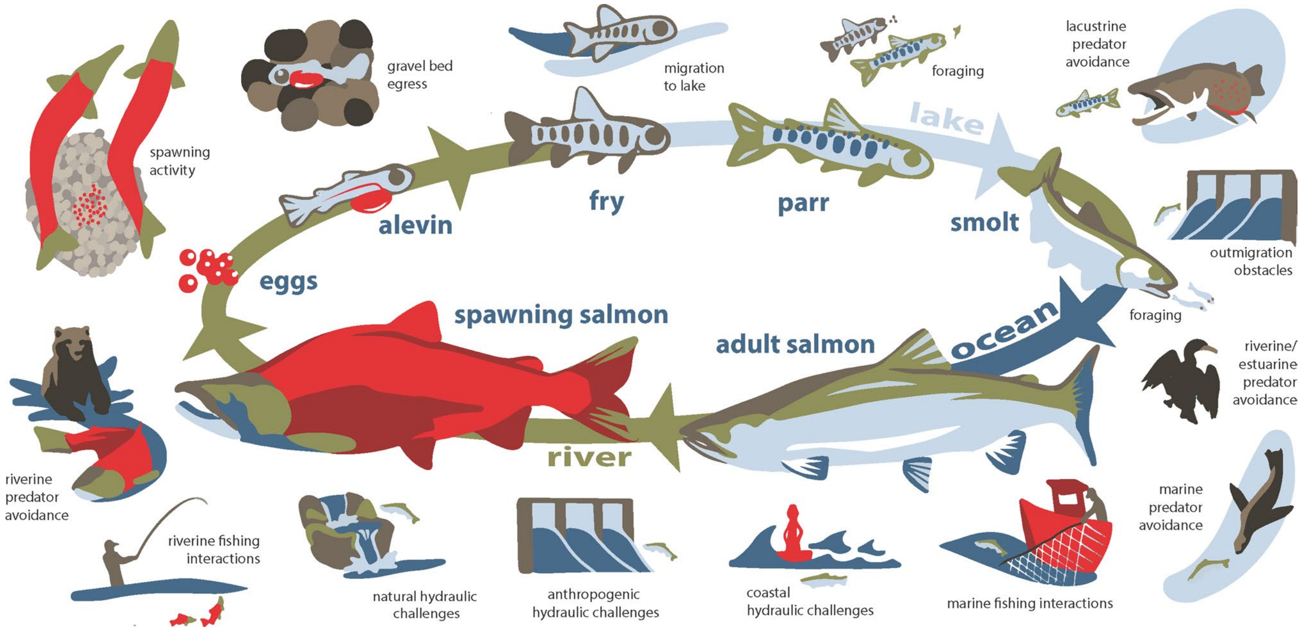

Figure 1. Anaerobic exercise across the Pacific salmon lifecycle.

abiotic factors may modify anaerobic demands and the subsequent responses to these demands.

3.1. Modifying factors

3.1.1. Increased temperature

Temperature is an important ecological factor, particularly for ectotherms, because it affects the physiology and ecology of fish, with wide ranging impacts on species fitness (Fry 1971). In fact, temperature has long been referred to as the "master factor" for the biology of fishes, dictating physiological processes on multiple biological levels (Brett 1971). Absolute aerobic scope [AAS, Absolute aerobic scope = maximum metabolic rate (MMR) – resting metabolic rate (RMR)] represents the aerobic capacity for a fish to perform activities beyond routine maintenance, such as swimming, digesting, and competing for mates. Aerobic performance is greatest at the optimal temperature (T_{opt}) for AAS, and declines outside of T_{opt}. The T_{opt} window may be narrow or wide, depending on species or populations, but tends to be narrow in Pacific salmon, which are stenotherms (Eliason et al. 2011). Peak summer temperatures across the west coast of North America have however increased significantly in recent years (Patterson et al. 2007), reaching critical limits for some populations (Eliason et al. 2011). This is forcing salmon to migrate at temperatures outside their T_{opt} range, and leading to mass mortality (Crossin et al. 2008; Martins et al. 2011; Crozier et al. 2021; Hinch et al. 2021). As temperatures increase and reach the critical temperature (T_{crit}), AAS becomes zero. This occurs when RMR intersects with MMR. At this temperature, survival is time-limited, and any further increase in temperature means life is supported solely by anaerobic metabolism (Pörtner and Farrell 2008). Of note is the fact that T_{opt} varies depending on the performance trait being measured; that is, the optimal temperature for AAS can differ from the optimal temperature for growth, digestion, immune function, reproduction and so on (Clark et al. 2013). Factorial aerobic scope [FAS, Factorial aerobic scope = MMR/RMR] evaluates aerobic capacity as a proportion of maintenance costs, and can reveal when a metabolic constraint may develop (Clark et al. 2013; Halsey et al. 2018; Eliason et al. 2022). As temperatures warm, FAS typically decreases (even if AAS is maintained). A low FAS indicates that fish are allocating most of their energy toward maintenance metabolism, and may not have sufficient remaining energy to support other fitness-enhancing activities (e.g., digestion of an average-sized meal in rainbow trout requires a minimum of FAS = 2; Eliason et al. 2008). While AAS may be most ecologically relevant for adult life stages because maximum metabolic capacity is critical to support swimming to reach distant spawning grounds, FAS may be particularly ecologically relevant for juvenile life stages because maximum metabolic capacity is not commonly utilized, but growth is critical.

As temperatures above T_{opt} cause a decline in aerobic (and cardiac) scope, fish can either become less active to avoid becoming anaerobic, or recruit anaerobic metabolic pathways to meet their energetic demands when performing activities exceeding their aerobic capacity. It is well established that salmonids increase their reliance on anaerobic swimming as they approach U_{crit} at supra-optimal temperatures (Brett 1964; Jain and Farrell 2003; Eliason et al. 2013a). For example, Eliason et al. (2013b) found that sockeye salmon exposed to high temperatures (22–26 °C) had elevated plasma lactate even at rest, and glucose depletion with swimming, providing evidence of compromised oxygen delivery to tissues and anaerobic metabolism. This temperature-induced mismatch between oxygen supply and demand can only temporarily be supported by anaerobic metabolism and prolonged exposure eventually becomes fatal.

There is ample evidence demonstrating impaired recovery in Pacific salmon with increasing temperature. For example, both males and females coho salmon had impaired recovery 1 hr post-exhaustive exercise at 18 °C compared to 14 °C, though an impairment was still noticeable at both temperatures 5 hr post-exhaustive exercise in males compared to females (Kraskura et al. 2020). A simulated fisheries capture also revealed that high temperatures alter the initial rate of cardiac recovery but not its duration (~10 hr) in sockeye salmon, suggesting that the rate of energy expenditure during recovery is elevated with temperature (Prystay et al. 2017). Similarly, Gale et al. (2011) also showed that sockeye salmon displayed loss of equilibrium following a simulated fisheries capture for much longer at high temperatures than at cooler temperatures. In many ways, increased temperature seems to intensify the physiological and behavioral effects of anaerobic exercise, with mortality being a common outcome. In contrast, because athletic performance in fish (e.g., U_{crit}, metabolic rates) is typically lower in cooler temperatures, the magnitude of physiological disturbance associated with anaerobic exercise will be lower, and so will the need for recovery. If the magnitude of the disturbance is the same however, it may actually take longer to recover in cold water due to reaction rates and a lower absolute aerobic scope at temperatures below T_{opt}.

3.1.2. Other modifying factors

There are many other factors that may alter both the requirement and capacity for anaerobic exercise and its subsequent physiological impacts in fish, but these have not been sufficiently studied to provide clarity on mechanisms or relationships. Low environmental oxygen (hypoxia) acts as a limiting factor on aerobic capacity (Richards et al. 2009). Hypoxia can be prevalent in crowded spawning grounds, gravel redds, nearshore marine environments, isolated freshwater pools, and during fisheries interactions. Under moderate hypoxia, salmon aerobic performance may be impaired, for example, digestion may be prolonged (Eliason and Farrell 2016) and development may be slowed (Del Rio et al. 2019). Under more extreme hypoxia however, there is insufficient oxygen available to meet demand, and thus fish must rely on anaerobic pathways for energy. Relatively few studies have specifically examined how hypoxia (moderate or extreme) impacts swimming and recovery in Pacific salmon. One study did show that moderately hypoxic conditions impaired recovery in mature sockeye salmon after an initial U_{crit} test, and most fish exposed to these conditions did not swim again and showed high plasma lactate (Farrell et al. 1998). Oldham et al. (2019) showed that 50% oxygen saturation—a level of oxygen frequently encountered in commercial aquaculture farms—reduced AAS and swimming performance in Atlantic salmon (*Salmo salar*), with smaller individuals achieving higher relative U_{crit} than larger individuals but experiencing a larger reduction (62%) in AAS, making smaller fish more susceptible to hypoxic conditions. Similar reductions in performance have been observed in rainbow trout as well (e.g., Jones 1971). As some habitats continue to become more hypoxic, or at least experience hypoxic conditions more frequently, a better understanding of the links between anaerobic exercise, recovery, and hypoxia is needed, particularly given that hypoxia is often encountered during fisheries interactions (e.g., crowding in seines, air exposure by recreational anglers for photos).

Contaminants are another form of modifying factors that may affect reliance on anaerobic metabolism, and a salmon's ability to recover. Two studies using mature sockeye salmon captured from the same population and location reported two different anaerobic recovery responses to contaminant exposure. The one study showed that a sub-lethal exposure to pentachlorophenol did not have significant impacts on swim performance and recovery (Farrell et al. 1998). In contrast, the second study showed exposure to dehydroabietic acid caused mature sockeye salmon to have a significantly elevated routine metabolic rate (compared to control fish) and significantly impaired recovery (Jain et al. 1998). Similarly, exposure to diluted bitumen (a heavy crude heavier than petroleum) reduced the swimming performance and AAS of juvenile sockeye salmon, and prolonged their post-exercise recovery (Lin et al. 2022).

Fish health status is also likely to impact the ability to perform anaerobically and to recover. Sockeye salmon in ill health did not differ in routine metabolic rate, but had lower post-exercise oxygen consumption and were unable to repeat their critical swim speed a second time (Tierney and Farrell 2004). The same study even suggested that a sockeye salmon's ability to recover quickly from exercise may be a useful indicator of health status. Another study on rainbow trout showed that blood consumption by sea lice—at a density of ≥0.5 sea lice g^{-1}—could cause anemia and decrease swimming performance (Wagner and McKinley 2004). Higher infection loads of sea lice on these fish would thus severely compound the osmotic balance issues already imposed by sea lice infections. The implications of fish health on ecophysiology have been increasingly appreciated in recent years, with studies having shown changes in metabolic rate, activity, and osmoregulation (e.g., Nadler et al. 2021; Chrétien et al. 2022). Within the context of salmonids, factors that increase pathogen transmission and result in higher pathogen loads, such as aquaculture/hatchery interactions with wild salmonids could have serious implications on their anaerobic performance, and their subsequent need and capacity to recover.

3.2. Natural events

3.2.1. Alevin and fry migrations

In Pacific salmon, directed movements begin at the alevin stage, first by moving deeper into the gravel following hatching, then by moving laterally through the gravel, and finally upward to emerge out of the gravel as fully formed fry once their maternally provided yolk-sac has been absorbed (Quinn 2018). The eggs can be buried deep under the gravel, and the initial downward movement occurs at high velocities (Fast 1987). Their movements also cause a build-up of carbon dioxide, which induces the alevins to move more in an effort to circulate water (Bams 1969). Although anaerobic exercise has not been studied in alevins, it is likely that they use burst swimming during the movements they undertake. Alevins have been shown to be rather sensitive to low levels of dissolved oxygen, and have several behavioral adaptations related to respiration (Fast 1987).

Once fry emerge from gravel redds following yolk-sac absorption, they immediately make their way to rearing areas, where they will feed and grow, typically for 1 to 2 years (Groot and Margolis 1991). Depending on the species, initial rearing areas may be within lakes (e.g., kokanee, most sockeye), streams and rivers (e.g., Chinook, coho, some sockeye), or even estuaries (e.g., pink & chum salmon). The direction of fry migration depends on the species and populations; some must migrate downstream to rearing areas (e.g., sockeye born in the inlet to a lake) while others must volitionally migrate upstream (e.g., sockeye born in the outlet to a lake) (Quinn and Brannon 1982; Pon et al. 2007; Quinn 2018). Given these inter- and intraspecific differences in the demands imposed on fry, variability in certain performance traits such as burst swimming is expected. While population differences in burst swimming performance have been found in sockeye fry, these did not correlate with the expected level of difficulty during fry migration (Sopinka et al. 2013).

In a different study, Pon et al. (2007) raised sockeye fry from two populations, one born in the inlet and one in the outlet of a lake, and tested their capacity for bursting. The findings indicated that outlet fry were larger and more laterally compressed, and had a burst swimming performance that was 31% better than the inlet fry. So, fry that must migrate upstream to rearing areas appear to have superior bursting performance to those that must migrate downstream (Pon et al. 2007). The size and morphology of outlet fry however, did not correlate to bursting ability. Similar to results from Sopinka et al. (2013), observed differences in burst swimming performance may reflect population differences in enzyme activity levels involved in anaerobism (e.g., lactate dehydrogenase, citrate synthase; Tsuyuki and Williscroft 1977; Patterson et al. 2004), or even the difficulty of upstream migration as adults (Sopinka et al. 2013). Specific performance traits selected for during upriver migration may be passed on from parents to offspring, and thus detectable in fry (Tierney et al. 2009; Sopinka et al. 2013). Such adaptations also appear to be detectable in sockeye parr (Eliason et al. 2017).

The importance of recovery during the alevin and fry stages is unclear given that few studies have explored these concepts. What is clear is that fish in both life stages are required to use anaerobic metabolism to support intense exercise, and as such must recover physiologically. For alevins, a failure to recover could mean dying in the gravel; if dissolved oxygen concentrations (i.e., hypoxia) or temperatures (high or low) exceed tolerances (e.g., Del Rio et al. 2019), and an individual is incapable of bursting to find suitable conditions because of a failure to recover, then death is inevitable. For some fry, an inability to burst means an inability to reach rearing habitats and potential vulnerability to predator attacks.

3.2.2. Foraging and escaping predators

It has been argued that population differences in burst swimming performance could also reflect differences in predation pressure (Bams 1967; Taylor and McPhail 1985), as evading predators requires bursting (and thus recovery). For example, Taylor and McPhail (1985) demonstrated that larger coho fry attained greater mean and maximum burst speeds than smaller conspecifics, and were more likely to evade a predator. The authors suggest that size-mediated differences in burst performance may be the basis for differences in predation susceptibility, given that smaller juvenile salmonids are more at risk of predation (Bams 1967). Fry must therefore recover rapidly from predation events to resume foraging quickly. This is particularly important given that rapid growth is linked to survival and fitness, and thus net energy intake must be maximized (Dill 1978).

Once fry reach their rearing areas, they must start to feed, and this too requires burst swimming. Young salmonids often feed on drifting invertebrates by swimming upstream from a stationary position to catch their prey, and tend to forage over short distances, particularly in high flow systems, to minimize the costs of foraging (i.e., the anaerobic costs of burst swimming; Godin and Rangeley 1989; Kemp et al. 2006). One study on Atlantic salmon parr demonstrated that foraging rate was independent of flow, but that high flows caused fish to utilize a smaller area of the experimental setup to minimize the costs of foraging (Kemp et al. 2006). Doing so reduced the distance the fish were required to burst, indicating that the energetic costs of foraging are large enough to provoke a sizable decline in performance (Kemp et al. 2006). In another study, coho fry were observed in their natural habitat, and tail beat frequency was calculated as the fish performed normal daily activities such as stationary swimming, free swimming, charging or feeding, as well as the speed and time spent performing each activity (Puckett and Dill 1985). These observations were then used to estimate the hourly energetic costs of each behavior for territorial and non-territorial fish. Territorial fish were found to spend 76% of their energy on stationary swimming, and 13% on feeding, while non-territorial fish spent 50% of their energy on stationary swimming, and 2% on feeding (Puckett and Dill 1985). In addition, the costs per feeding “motion” were lower for territorial fish than for non-territorial fish, suggesting that territoriality reduces the costs of foraging, either by 1) reducing search costs by minimizing the foraging distance (Godin and Rangeley 1989), or 2) reducing bursting costs in pursuit of prey, particularly if territorial fish are better burst swimmers (Puckett and Dill 1985). These studies did not directly explore anaerobic activities but provide some data to support the idea that anaerobic bursting is required to forage and escape territorial conspecifics.

Foraging and escaping predators require burst swimming and the recruitment of anaerobic metabolic pathways, regardless of the life stage. Because studies on fish at sea are logistically challenging, bursting has not been studied in sub-adults and adults in the marine environment, where most somatic growth occurs and where predation can be high. As technology continues to evolve, electronic tags may offer an avenue for future research to address this knowledge gap. To date however, recovery from foraging or predation events has not been directly investigated. In fact, how much bursting is required to feed vs. escape various predators at each life stage is not known. Importantly, foraging may require a single burst of activity, but evading predators may require multiple bursts. For example, if a predator attacks more than once in close succession, recovery from the first attempt is unlikely to be complete by the time the second attempt occurs. Following successful foraging, both digestion and recovery are required, and both take up part of the available AAS (Beamish 1978; Eliason and Farrell 2016). During digestion, recovery could be compromised, and it remains unclear which process is prioritized in terms of energy use. Chinook salmon (life stage not reported) exercised at high speeds for 8 months were able to maintain a similar growth rate to those exercised at lower speeds by increasing hematocrit and thus maintaining oxygen delivery to the intestines (Thorarensen et al. 1993). So, fish could perhaps maintain digestive capacity while recovering but these nuances have not yet been explored, and could contribute to mortality if this ability only arises upon long-term exercise, or in specific life stages.

3.2.3. Spawning migration

Pacific salmon return migrations begin at sea, when their directed movements toward their natal river starts, though much more research has been devoted to studying riverine movements. One recent study on Fraser River sockeye salmon used accelerometers to assess field metabolic rates and found that oxygen consumption rates were twice as high in the river as they were in coastal regions, but the cost of transport was highest in Seymour Narrows, a narrow coastal region with high tidal flushing (Wilson et al. 2022).

The finding highlights that the coastal marine migration is likely an important component of the spawning migration energy budget of Pacific salmon. The same study found that acceleration values >3.0 m s^{-2}, representing bursting behavior, were rarely observed, but were more frequently observed in the river than in the marine environment.

During upriver migration, many Pacific salmon must overcome severe hydraulic challenges. For Fraser River salmon, one of these challenges is Hell's Gate, a notoriously difficult reach located 180 km upstream of the estuary (Macdonald and Williams 1998; Hinch and Bratty 2000). Fishways were constructed on both sides of the river in some segments of Hell's Gate to mitigate issues with passage (Clay 1995), but average swimming speeds are still higher at this location than anywhere else in the Fraser Canyon where fish were tracked (Hinch et al. 1996; Hinch and Rand 1998). Several studies have confirmed that anaerobic white muscles are recruited for passing this stretch (Hinch et al. 1996). Subsequent research using electromyogram telemetry also revealed that sockeye salmon that successfully overcame Hell's Gate never exceeded Ucrit for more than 3 min, while unsuccessful individuals sometimes exceeded Ucrit for >10 min (Hinch and Bratty 2000). Macdonald (2000) also showed that Early Stuart sockeye salmon cannot successfully make it upstream to their spawning grounds in years with extremely high flows. Chum salmon from the Haraki River (Japan) did not exhibit spawning behavior during heavy flow, instead spending most of their time holding downstream (Tsuda et al. 2006). Chinook salmon from the Klickitat River (Washington) tagged with electromyogram (EMG) transmitters swam above their critical swimming speeds a greater proportion of the time while overcoming three waterfalls than between the waterfalls (58.9% vs. 1.7%; Brown and Geist 2002). Energy expenditure appeared to be greater when swimming between the falls however than when ascending the falls, perhaps in part because the cost of recovery was high. Collectively, these studies support the idea that naturally high flows can be prohibitively challenging for salmon, and that excessive utilization of anaerobic metabolism during these challenges can lead to migration failure and ultimately be fatal for adult salmon (Godfrey et al. 1954; Makiguchi et al. 2007, 2011).

During their spawning migration, Pacific salmon must burst repeatedly. Although evidence suggest a need for ~50% recovery before swimming at their critical speed again (i.e., repeat swim performance; Kraskura et al. 2020), it remains unclear how much recovery is required between short bursts that may require swimming below critical swim speeds. This "refractory period" is likely an important determinant of success for salmon. This is also particularly relevant within the context of spawning activity, fisheries interactions and hydraulic challenges when multiple bursts of activity in close succession are likely frequent.

3.2.4. On the spawning grounds

There has been relatively little effort to study swimming and metabolism on the spawning grounds, perhaps because salmon are most "hardy" at that point—their scales resorb and their bodies harden (Raby et al. 2013). Thus, there is presumably an assumption that once fish have reached their spawning grounds, they are likely to successfully reproduce. In other words, the research questions of critical importance for conservation and management purposes are generally linked to the difficulties encountered during upstream migration (e.g., Patterson et al. 2016), and less so once on the spawning grounds. Salmon are still faced with challenges on the spawning grounds however, which could affect their survival *via* links to metabolism (and other pathways), including for example injuries (Bass et al. 2018) and pathogens (Miller et al. 2011).

Within salmonids, specific spawning behaviors are conserved across species, including digging, covering, oviposition and aggression (Needham and Taft 1934; Tautz and Groot 1975). Females choose a location for their redd where flow conditions are optimal, and may fight for access to the best site. Once their site is chosen, they beat their tails against the substrate (digging) to clear fine sediments. Females then use their anal fin to probe the substrate before depositing their eggs (oviposition). During oviposition, males position themselves alongside females and quiver, and subsequently release milt. Females then immediately cover their eggs using rapid tail beats. This cycle of digging, oviposition and covering occurs several times (sometimes over days) until the female has deposited all her eggs (Needham and Taft 1934; Orcutt et al. 1968; Tautz and Groot 1975). Before, during and often after spawning, males display aggression to access mates. There is rich literature describing these behaviors on the spawning grounds from observational studies, but few have quantified behaviors and their aerobic *vs* anaerobic energetic costs (see exceptions Healey et al. 2003; Fuchs and Caudill 2019). None that the authors are aware of have quantified the need for recovery during spawning.

It is well known however, that spawning behaviors are costly. The majority of these costs is due to aerobic activities, mostly related to holding and the continuous investment in ripening gonads. Populations of *O. nerka* and *O. gorbuscha* with longer migrations enter freshwater with higher gross somatic energy than those with shorter migrations (with females having generally higher gross somatic energy than males) (see Eliason and Farrell 2016 for summary). In all cases, the energy spent during spawning represents a sizable proportion of the total energy expenditure, and as such poor energy allocation during migration will have profound impacts on reproductive success (Eliason and Farrell 2016 and references therein). On the spawning grounds, dominant males tend to expend the most energy each day, with satellite males expending nearly as much, but females expending considerably less (chum salmon; McVeigh et al. 2007). When compared to known data from Early Stuart sockeye salmon, Kanaka chum salmon arrived to the spawning grounds with less somatic energy, but died with approximately the same amount as Early Stuart sockeye, suggesting lower energy expenditure on the spawning grounds in chum salmon (McVeigh et al. 2007). In Early Stuart sockeye salmon, dominant males and spawning females spent considerably more energy every day than subordinate males and guarding females (Healey et al. 2003). Overall, these findings suggest that the cost of spawning is largely due to aerobic costs, but that behaviors associated with spawning still require anaerobic swimming.

Recent advances in biologging and biotelemetry technology have enabled measurements of heart rate and acceleration (or jerk—rate of change of acceleration—typically reported in *g* force) from free-swimming fish, and has shown strong relationships between acceleration, heart rate, tail beat frequency and energy expenditure (e.g., Clark et al. 2010). For example, Prystay et al. (2020) explored the relationship between heart rate and dominance behavior on the spawning grounds, and found no correlation between the two. Instead, routine heart rate was linked to temperature, and seemed to be lower at night, though this observation became less pronounced as the spawning period progressed. Similarly, heart rate was highly influenced by temperature in spawning Chinook salmon, and scope for heart rate was greater in wild fish than hatchery-reared individuals (Twardek et al. 2021). EMG telemetry also accurately described specific spawning events in female Chinook (Berejikian et al. 2007). More recently, Fuchs and Caudill (2019) used accelerometer tags to link jerk data to specific spawning behaviors. Specifically, female steelhead trout reached jerks of 1.5 *g* during digging and covering behaviors (with minimum jerks of 0.9 *g* during these behaviors) (Fuchs and Caudill 2019). Male steelhead trout reached lower maximum jerk than females, with aggression being the most intense behavior. In comparison, 1–2.5 s bursts, lateral movements and oviposition (females only) generally yielded jerks of less than 0.5 *g*, and were thus likely to be less energetically and aerobically costly. Holding behavior yielded the lowest jerk (~0.1 *g*) (Fuchs and Caudill 2019). Thus, accelerometers can be used to quantify detailed time and energy budgets of animals, and may suggest that anaerobic exercise is used on the spawning grounds, particularly in females, when digging and covering redds. Because steelhead trout tend to be less densely packed on spawning grounds than most other Pacific salmon, more bursting and anaerobic swimming in species like sockeye salmon may be expected, as they aggregate by the thousands over relatively small spawning grounds, and must therefore be more aggressive.

3.3. Anthropogenic challenges

3.3.1. Fisheries interactions

Pacific salmon are common targets and bycatch for recreational anglers, Indigenous, and commercial fisheries (Baker and Schindler 2009; Department of Fisheries and Oceans Canada 2010). Fishing methods include purse seining, beach seining, gill netting, traps, trolling, and rod-and-reel fishing, each eliciting different levels of bursting, and exposing fish to different levels of crowding, air exposure and injury. Fisheries-induced physiological stressors can result from hooking, landing, handling and entanglement, but also from the increased heart rate, exhaustive exercise and air exposure associated with such interactions (Davis 2010). Because fish rely on anaerobic pathways during exhaustive exercise and hypoxia, anaerobic metabolism is an inevitable response to fisheries interactions (Cooke et al. 2012). These interactions can result in various durations of hypoxia and exhaustive exercise, ranging from seconds to minutes (Brownscombe et al. 2017). For example, ventilation may be physically restricted in net or shore seine fisheries, or a fight on hook-and-line may lead to exhaustion. Given that, the need to understand the consequences of such interactions has led to a range of studies exploring how salmon fare during and after a fisheries' encounter (reviewed in Patterson et al. 2017a).

Several studies have found that increased air exposure had the greatest impact on the survival of non-target species, suggesting that air exposure is a severe form of acute stress (Humborstad et al. 2009;

Benoît et al. 2010; Cook et al. 2015, 2018a). Cook et al. (2018a) used an experimental approach to evaluate the response of chum salmon (*O. keta*) to capture stressors implicated in commercial purse seine fisheries. Specifically, the authors investigated thresholds in physiological responses to duration spent in purse seine and duration of air exposure. They found that indicators of physiological exhaustion increased with time pursed, where 15 min was identified as an important transition point, likely reflecting the limit after which anaerobic exercise fails to meet metabolic demands (Cook et al. 2015). Air exposures of 1 to 3 min detrimentally affected survival, while air exposures exceeding 6 min resulted in physiological exhaustion, with an inability to mobilize glucose readily (Cook et al. 2018a). Studies investigating the effects of fisheries interactions have generally found an increase in plasma chloride and sodium (Gale et al. 2011; Cook et al. 2015, 2018a), reflecting osmotic disturbances from anaerobic exercise (Wood and Randall 1973a, 1973b; Wood 1991). These disturbances are exacerbated in seawater, owing to the osmo-respiratory compromise of the fish gill (Wood 2022).

In a series of studies on sockeye salmon (Gale et al. 2011, 2014), the effects of exhaustive exercise and air exposure were investigated under different ecologically relevant temperatures. In addition to increased lactate, chloride, sodium and osmolality following 3 min of exhaustive exercise (for up to 72 hr post-exposure), the authors found that an additional 1 min of air exposure elevated glucose in females only, and exacerbated high lactate levels. All air-exposed fish in the warmest treatment group failed to maintain equilibrium once returned to the water, suggesting that high temperatures exacerbate the effects of exhaustive exercise. In fact, temperature and sex were the best predictor for survival 24 hr and 48 hr post-treatment (Gale et al. 2014). Air exposure further caused a decline in ventilation rates post-exercise, and this decline was significantly greater in the warm treatment. This means that the fish with the highest oxygen debt, and the greatest need to recover oxygen, were the least able to do so quickly. In another study, Donaldson et al. (2010) explored the impacts of different duration of corralling (simulating fisheries gear) on heart rate and found that while maximum heart rate was the same whether fish were corralled for 10 or 30 min, the fish in the longer duration treatment took significantly longer to recover their heart rate to pre-corralling levels. The response to and recovery from fisheries-induced stressors can vary across species and individuals depending on factors such as body size and reproductive status (Donaldson et al. 2010, 2012, 2014; Raby et al. 2013), but also depending on the environmental conditions to which the fish are exposed at the time of capture (Gale et al. 2011, 2013, 2014; Robinson et al. 2013).

3.3.2. Anthropogenic hydraulic challenges

Hydraulically complex and challenging flow regimes associated with man-made barriers can cause confusion, incur delays, hamper passage, as well as cause physiological stress and increase energy expenditure (Keefer et al. 2004; Naughton et al. 2005; Rand et al. 2006; Caudill et al. 2007; Nadeau et al. 2010). Many studies have linked flow dynamics to swimming activity, behavior and energy expenditure of wild Pacific salmon (e.g., Brown et al. 2006; Pon et al. 2009a, 2009b; Burnett et al. 2014a, Burnett et al. 2014b; Li et al. 2021). Salmon exhibit burst swimming to overcome fast flows, recruiting anaerobic pathways to do so. For example, Chinook salmon (*O. tshawytscha*) swam above their Ucrit in the Bonneville Dam tailrace (Brown et al. 2006). Using acoustic accelerometer tags, Burnett et al. (2014b) found that sockeye salmon (*O. nerka*) that elicited excessive amounts of burst swimming were more likely to die following fishway passage through Seton Dam. More specifically, fish that experienced higher flows and high water shear stress during their passage recruited anaerobic pathways more often *and* were more likely to experience delayed mortality. In addition, females swam anaerobically more often than males, were 5–9% less likely to pass the dam, and were 21–31% less likely to survive to spawning grounds (Burnett et al. 2014a, 2014b; Li et al. 2021). Sockeye salmon made to pass the Seton Dam fishway a second time were significantly more likely to die in the two lakes upstream of the dam than fish that only had to pass once, suggesting delayed consequences from repeating this challenge and the failure to fully recover from the first anaerobic event (Roscoe et al. 2011; Burnett et al. 2014b). Rainbow trout from the American River (California) showed increased swim speeds and increased oxygen consumption rates during the increasing flow stage of a hydroelectric-power-generation-related pulsed-flow sequence (Cocherell et al. 2011). The same study found lower speeds at peak flows, and the authors suggest that this is due to the fish using the river's habitat heterogeneities as hydraulic cover. The need to recover from bouts of bursting could also underlie the need to lower swim speeds and use of hydraulic refuge.

4. What happens during recovery?

Recovery from anaerobic activity requires both time and energy. Both of these components represent costs to the fish. A prolonged time for recovery could result in delayed migration (Caudill et al. 2007), opportunity costs (e.g., competing for mates, territory, foraging), and increased susceptibility to predation. Excessive energy allocated to recovery could deplete finite energy stores (in adult migrating salmon, Rand et al. 2006), squander resources that could be allocated for growth in other life stages, and increase susceptibility to disease. The energetic cost of recovery, in terms of oxygen debt, is termed the EPOC, and this is calculated by measuring the total oxygen consumed during the recovery period (minus baseline maintenance metabolism; Lee et al. 2003; Zhang et al. 2018; Figure 2). EPOC does not consider the costs of recovery in terms of endogenous energy stores, an aspect of recovery that has not yet been fully explored.

There are multiple phases of recovery from exercise. During the initial, rapid phase of EPOC, fish are particular vulnerable because they may be refractory to any exercise stimuli (i.e., they cannot swim at all) if they were fully exhausted (e.g., following an angling event). The initial phase of recovery is characterized by a rapid decrease in circulating catecholamines and increase in muscle PCr and ATP (Milligan 1996, Scarabello et al. 1991a, 1991b; Eliason et al. 2020). The duration of this initial EPOC phase is expected to vary with the intensity of the burst exercise as well as biotic (e.g., life stage, species) and abiotic (e.g., temperature, dissolved oxygen) factors but typically resolves within an hour. Salmon do not need to fully recover to RMR or pre-exercise

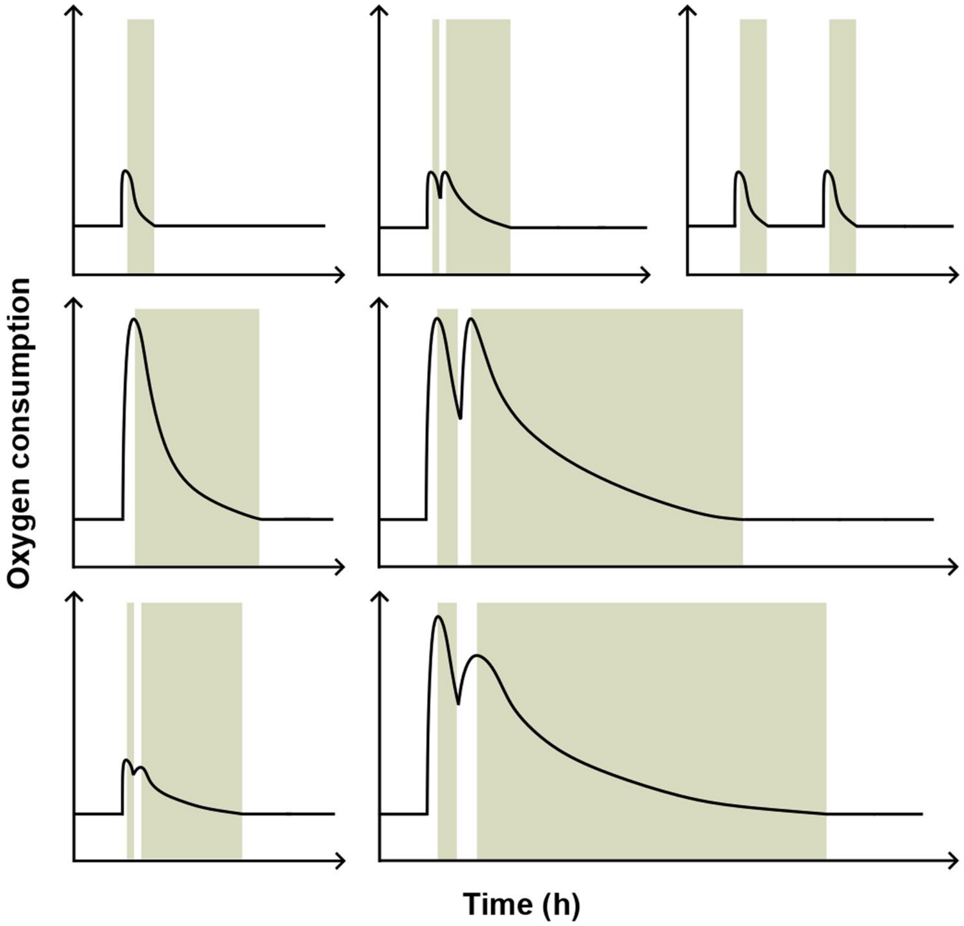

Figure 2. Schematic of the hypothesized duration of recovery (shaded boxes) depending on the type and duration of burst swimming (lines). (A) A short burst, followed by a fast recovery. (B) Two short bursts, without full recovery in between, with a subsequent longer recovery. (C) Two short bursts, with full recovery after each. (D) One long burst, followed by a longer recovery. (E) Two long bursts, without full recovery in between, followed by a very long recovery. (F) One short burst, followed by another burst with too little time for recovery in between, so the fish is incapable of properly bursting. (G) One long burst, followed by another burst with too little time for recovery in between, so the fish is incapable of properly bursting. Note that this figure is purely illustrative; the interplay between the type/duration of burst swimming and the duration of recovery is a significant knowledge gap in the field, and requires more data.

cardiovascular levels before resuming swimming (Farrell et al. 1998; Farrell and Clutterham 2003; Eliason et al. 2013b). Although it may be ideal to express % recovery in relation to SMR and AAS (see Zhang et al. 2018), this is not always practical for studies where SMR cannot be measured (e.g., sexually mature adult salmon, studies with swim tunnels). Work with adult salmon suggests that under optimal temperatures, salmon can repeat swim performance (or in the wild, presumably resume migration or other normal swimming behaviors) once they recover to ~50% of their MMR (Kraskura et al. 2020).

During the second, slower phase of EPOC, oxygen consumption continues to decline back down to baseline, routine levels (Table 1) and the remaining ionic, metabolite and hormonal imbalances described in Section 3 resolve (Figure 3). Plasma cortisol typically peaks after 1–2 hr of recovery and declines to baseline levels more rapidly for adult males but remains elevated for a prolonged duration for female salmon (e.g., Eliason et al. 2020). Muscle lactate slowly declines over time, while plasma lactate peaks ~30 min to 3 hr after exercise (depending on species, and environment; Parker et al. 1959; Milligan 1996). See Milligan (1996) and Zhang et al. (2018) for a summary of metabolites and recovery dynamics. Across studies and salmon life stages, recovery duration can range from less than 1 hr to upwards to 12 hr, depending on the species and method used (Table 1). Notably, this 12-hr recovery period is referring to healthy salmonids, and typically in freshwater. Recovery from exhaustive exercise can be substantially longer in seawater, as shown in Atlantic salmon (Hvas et al. 2020a, 2021b) and coho (Parker et al. 1959) due to the need for osmotic recovery. Also of note is the fact that wild salmon may not exhibit a "classic" recovery profile, which may make the second phase and energetic cost of full EPOC challenging to estimate. For example, adult coho salmon exhibited heightened activity throughout recovery (Kraskura et al. 2020), possibly because of the spawning life stage. Heart rate is particularly sensitive to stressors and may be the most effective metric to determine when recovery is complete (Prystay et al. 2017), particularly in a field setting (Prystay et al. 2020; Hvas et al. 2020b; Twardek et al. 2021).

Cortisol is a key hormone in the stress response in fish; however, excess cortisol may have a negative impact on the ability of salmon to rapidly recover from an exhaustive stressor. This is particularly alarming for adult salmon because female adult salmon are known to have elevated circulating levels of plasma cortisol and a prolonged cortisol response to a stressor (Schmidt and Idler 1962; Hruska et al. 2010; Gale et al. 2011; Jeffries et al. 2012; Eliason et al. 2020). Cortisol responses are often studied in

Table 1. Duration of recovery in Pacific salmon following exhaustive exercise.

Species	Origin	Type of exercise	Method of assessment	Duration of recovery	Reference
Coho salmon (adults)	Chehalis River, British Columbia, Canada	Acute thermal challenge and capture event	Static respirometry & blood chemistry	Small males (jacks): 9.3 hr Full-sized males: 12.3 hr	Clark et al. (2012)
Summer-run sockeye salmon (adults)	Fraser River, British Columbia, Canada	Catch and release fishery, combined with high temperature	Heart rate loggers	10 hr	Prystay et al. (2017)
Coho and sockeye salmon (adults)	Chehalis River and Fraser River, British Columbia, Canada	Continuous swimming to fatigue	Swim tunnel respirometry	0.8 hr	Lee et al. (2003)
Sockeye (juveniles)	Lab-reared (unreported origin)	Continuous swimming to fatigue	Swim tunnel respirometry	4–5 hr	Brett (1964)
Rainbow trout (juveniles)	Hatchery-reared, Ontario, Canada	Chase for 3 min to exhaustion	Intermittent flow respirometry	3.5–6 hr	Scarabello et al. (1991a, 1991b, 1992)
Coho salmon (adults)	Chilliwack River, British Columbia, Canada	3 min chase + 1 min air exposure, simulating angling event	Intermittent flow respirometry	6.06 ± 0.35 hr	Kraskura et al. (2020)
Summer-run sockeye salmon (adults)	Lake Stuart/Stellako, Chilko and Quesnel stocks, Fraser River, British Columbia, Canada	3 min chase + 1 min air exposure, simulating angling event	Blood chemistry	≤72 hr	Gale et al. (2011)
Sockeye salmon (adults)	Harrison River, British Columbia, Canada	Beach seine + 3 min air exposure	Reflex impairments	1–2 hr	Raby et al. (2015)
Rainbow trout (adults)	Fish farm, Japan	Elastic binding to simulate net entanglement	Blood chemistry	≥6 hr	Kojima et al. (2004)
Rainbow trout (adults)	Tongariro River, New Zealand	Angling capture	Blood chemistry	≤24 hr	Pankhurst and Dedual (1994)

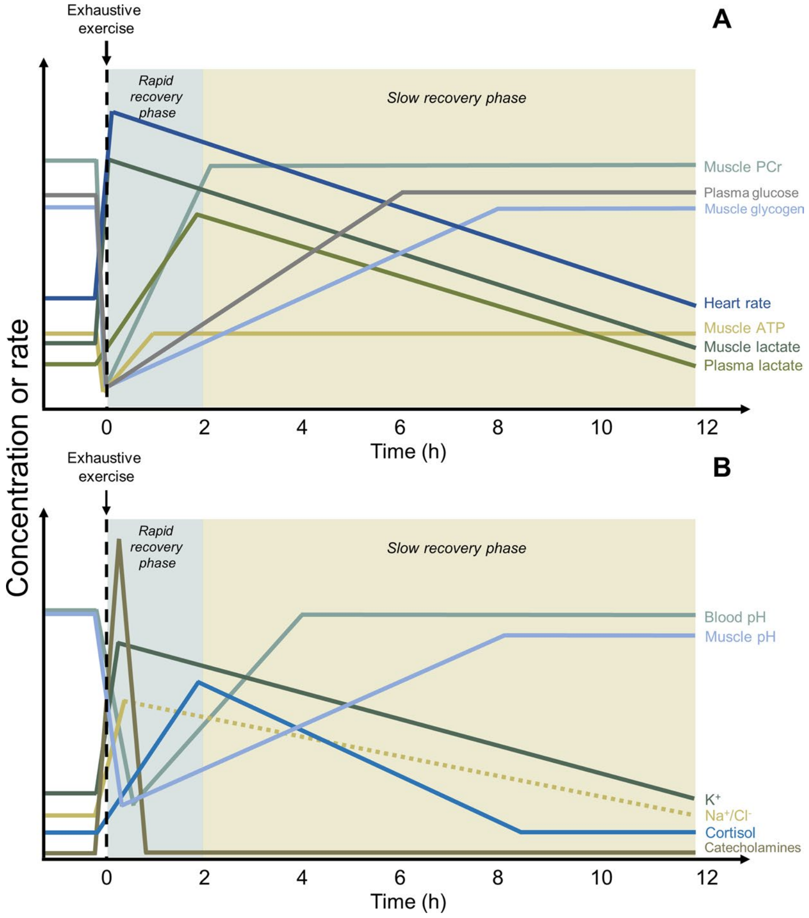

Figure 3. Schematic for recovery of (A) heart rate and metabolites, and (B) hormones, pH and ions following exhaustive exercise. These generalizations may not apply in all contexts. Modified from Zhang et al. (2018).

the lab however, so the stress of handling may exacerbate the cortisol response; the post-exercise cortisol response detected in many studies may therefore not be entirely due to the exercise event. In a study by Milligan (2003), rainbow trout were injected with either saline (control) or metyrapone (which blocks the synthesis of cortisol) 1 hr prior to exercise. Following exercise, half of the metyrapone-treated fish were injected with cortisol. The results indicated that metyrapone blocked the post-exercise elevation of cortisol, while the cortisol-treated fish had a higher cortisol increase than control fish. Glycogen stores were completely restored in metyrapone-treated fish within 2 hr post-exercise, partially restored in control fish after 4 hr, but not restored at all in cortisol-treated fish (Milligan 2003). The exact mechanism by which cortisol inhibits glycogen resynthesis is not fully understood however. In another similar study, elevated cortisol levels were associated with prolonged lactate recovery dynamics in rainbow trout (Pagnotta et al. 1994). Thus, elevated cortisol appears to both impair lactate and glycogen recovery following exercise, and likely plays a critical role in determining both the cost and duration of recovery in Pacific salmon.

5. Facilitating recovery: what can be done?

An important question within the context of recovery is: What can be done? Some of these metabolic consequences *can* in fact be mitigated by reducing anaerobic burden. For example, reducing the flow in spillways at hydroelectric dams will decrease the bursting effort required to overcome the dam, and thus lower anaerobic and recovery costs (Burnett et al. 2014a; Harrower et al. 2019). Catch-and-release fisheries could be closed during high temperatures (e.g. Van Leeuwen et al. 2021), when fish are already reverting to anaerobic metabolism and most definitely cannot cope with additional anaerobic burden (Gale et al. 2011; Cook et al. 2015, 2018a; Patterson et al. 2017a). Importantly, what constitutes high temperatures may vary depending on populations (Eliason et al. 2011), so there is a need to determine population-specific temperature thresholds. In addition, these temperature thresholds will likely vary (and be lower) if fish are simultaneously coping with fisheries stressors, so there is a need to assess thermal thresholds *within* the context of fisheries interactions. Certain fishing practices could also be changed during warm temperatures, where, for example, purse seining could be done over shorter periods of time to reduce the time that Pacific salmon bycatch spend in the net (Cook et al. 2018b). If release bycatch is intended as a conservation measure, then the increased probability of delayed mortality should be considered in management schemes (see Patterson et al. 2017b).

Many studies have also explored means of assisting fish in their recovery from fisheries interactions with the intention to increase post-release survival. Robinson et al. (2013) mimicked a method commonly used by recreational anglers, where salmon are held facing the current to promote ventilation with freshwater. Despite better survival at 16 °C than at 21 °C (all fish died within 3 days in the 21 °C), Fraser River sockeye that were assisted did not survive more than non-assisted fish. In fact, female survival at 16 °C was poorer after the ventilation assistance compared with the unassisted and control groups (Robinson et al. 2013). Other methods of assistance have however shown good results. The recovery box (or Fraser box) was used to successful revive >90% of coho salmon that appeared lethargic after being caught as bycatch in gillnet fisheries in the marine environment (Farrell et al. 2001), however whether fish completely recovered and survived to spawn is unknown. Following capture, fishers can put bycatch coho in a recovery box for 1 to 2 hr, with flow directed over their gills, thereby “saving” the fish, which can be subsequently released with good survival outcomes (Farrell et al. 2001). Such low velocity swimming appeared to aid in recovery, at least in experimental studies (Milligan et al. 2000; Farrell et al. 2001). Similar revival boxes in the river showed mixed results, but were successful in reviving moribund sockeye salmon after capture by seine and a 3-min air exposure (Nguyen et al. 2014; Raby et al. 2015). Fish already vigorous after capture did not benefit from such revival treatment however (Nguyen et al. 2014), so the benefits of aiding in recovery following capture should be tempered with the potential added stress of further handling or confinement (Raby et al. 2015). In particular, vigorous fish should always be immediately released.

Others ways of mitigating anaerobic exercise and the need for recovery include habitat restoration that offers predator and thermal refugia, as well as improved water quality that could also facilitate recovery given that several pollutants have been linked with impaired swim performance and recovery (Jain et al. 1998; Li et al. 2021). Limiting human activities and interactions at sensitive locations and life stages may also reduce the use of anaerobic exercise, and the subsequent need to recover.

Of course, when asking what can be done about recovery, the fact that physiological recovery is not fully understood within the field should not be overlooked. The mechanisms that underlie recovery, or that cause fish to die following exhaustive exercise remain an important knowledge gap (Holder et al. 2022). Within this context, more focused research attempting to address this knowledge gap could help us promote recovery in wild fishes and mitigate mortality resulting from recovery failure.

6. Pressing questions: when and why salmon fail to recover, and its implications

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC, Canada) and the National Oceanic and Atmospheric Administration (NOAA, USA) have assessed multiple populations of Pacific salmon, and determined that many are endangered, threatened or of special concern. For example, out of 24 designatable units of Fraser sockeye salmon, only 8 are considered not at risk (COSEWIC 2020a). In the USA, NOAA’s 2022 5-year review showed that 2 populations of Chinook are considered endangered, 7 are threatened, and 1 is currently being considered for listing. Similarly, steelhead are not faring well across their range (COSEWIC 2020b; see www.noaa.gov). Difficulties faced during upstream spawning migrations (high flows, increased temperature) and fisheries interactions pose significant challenges to Pacific salmon populations. This review has clearly demonstrated that these instances require fish to swim anaerobically, and that the need for recovery during this time is imperative for survival.

If populations of Pacific salmon are to be effectively managed, then it would help to first determine the threats they face, and when they are most sensitive to these threats (i.e., what life stage). This review argues that a failure to recover from exhaustive exercise is likely an important cause of mortality in Pacific salmon, but it remains unclear whether some species, populations, life stages or body sizes are more susceptible to this. Sockeye salmon have been studied far more than any other species, followed by Chinook. Coho, pink and chum salmon have not received the same attention, so relatively little is known about their anaerobic and recovery capacities, though there is evidence that pink salmon perform surprisingly well at warm temperatures, perhaps making them more resilient to climate change than other Pacific salmonids (Clark et al. 2011). Work on early life stages has been especially neglected in this realm, with most research focused on upstream migrating adults, so there is a need to assess anaerobic and recovery demands at the alevin, fry, parr, smolt and sub-adult stages. How can conservation and management actions be focused on the most sensitive individuals and populations if their sensitivity has not been assessed? Hill (1983) said that "one reason to focus on the physiology of juveniles and nestlings is that for many individuals it is the only physiology ever experienced". Early life stages experience significant mortality rates, but climate change has been an unfortunate game changer for migrating adult salmon, with adults now also experiencing high rates of mortality. Eggs, alevins, marine life stages and the spawning ground life stages are likely less affected by warming temperatures because they are typically associated with cooler temperatures. In these cases, the impacts of temperature on anaerobic activities and subsequent recovery are likely negligible, though they remain unexplored. This is not always the case however, as seen for California populations at the southern end of their range, which seem to be threatened by warm temperatures across their entire lifecycle (Crozier et al. 2021). Given what is known, exhaustive exercise associated with increased river flow and temperature during upriver migration of adults can be an important agent of mortality, particularly for summer-migrating populations. Migrating adults of these summer populations are likely the most reliant on anaerobic metabolism, and yet may have the least ability to recover. The freshwater rearing life stages (fry, parr, smolts) are also likely to be deeply affected by warming rivers, but there is a paucity of information in this realm. The collection of this data is imperative.

There is some evidence that larger individuals may be more at risk from anaerobic challenges. Clark et al. (2012) showed that smaller male coho salmon ("jacks") had lower increases in blood potassium following an acute thermal challenge than full-sized males. Additionally, metabolic recovery following exhaustive exercise was significantly faster in jacks, with recovery taking approximately 9.4 hr as opposed to 12.4 hr in full-sized males. Thus, larger fish accumulated a proportionally greater oxygen debt from anaerobic metabolism, which took longer to pay back. In a different study, the two largest individuals had reduced arterial oxygen saturation with warming, indicating that these fish could develop an oxygen limitation and rely more on anaerobic metabolism as temperatures warm (Clark et al. 2008). These findings not only suggest that larger individuals may be more at risk following a metabolic stressor, but also support the idea that non-lethal environmental and anthropogenic interactions that result in exhaustive exercise may select for smaller individuals over time due to an inability for larger fish to recover (Clark et al. 2012). It remains unknown at this time whether this is also the case across species, populations and life stages, so more research is necessary to assess whether larger fish are broadly at risk.

Adult female Pacific salmon experience mortality rates of up to 8-fold greater than males under stressful experimental conditions, with this mortality being most evident during upriver migration (average 2.1-fold; reviewed in Hinch et al. 2021). Mortality in females appeared to be particularly high when conditions were most challenging, for example when facing high flows, high temperatures or handling stressors, which are known to activate anaerobic metabolism, and require recovery (Hinch et al. 2021). There is mounting evidence that females have reduced capacity to physiologically recover, with levels of potassium and lactate remaining high >4 hr post-exercise (Eliason et al. 2020). Thus, recovery duration appears prolonged in some females, perhaps mediated *via* their chronically high cortisol levels (Sandblom et al. 2009; Eliason et al. 2020). Kraskura et al. (2020) did however find that while recovery was clearly impaired at high temperatures for both sexes, recovery was longer and more costly in male coho salmon than in females. Thus, the energetics of aerobic metabolism and recovery do not appear to explain increased mortality in female coho, and behavioral differences may be at play here. Studies that bridge physiological estimates of anaerobic exercise and recovery profiles with behavioral data would greatly advance the field by bringing together aspects of physiology and ecology. It also remains unclear whether differences between sexes exist among life stages other than maturing adults.

The mechanisms behind impaired recovery, and how these lead to death in Pacific salmon, and fishes more generally, are not fully understood (Holder et al. 2022). So, one of the most important questions to address within this context is: Is there a threshold for anaerobic exercise that does allow fish to survive? In other words, how much bursting is "too much"? Is there a threshold for plasma lactate concentration indicative of mortality? A threshold of 10-13mmol L^{-1} has been suggested as the point after which swimming performance and recovery become impaired, and at which mortality is likely to occur (Stevens and Black 1966; Farrell et al. 1998; Jain and Farrell 2003;

Crossin et al. 2009; Gale et al. 2014). At this point however, such physiological thresholds remain unknown and should be explored further. Important knowledge gaps also exist when it comes to the duration and intensity of anaerobic events, as well as the impacts of single events vs. multiple events. The most recent simulated exhaustive exercise tests rely on a 3-min chase and 1–3 min of air exposure, rather than the 15-min high-intensity chase used by Black (1957b) and Parker et al. (1959). Across their lifecycle, salmon are often required to burst multiple times in close succession, be it to avoid predation, forage or while overcoming hydraulic challenges. Each burst may vary in duration and intensity, so the subsequent need for recovery will also vary in duration and intensity. These nuances need to be explored further to predict the consequences of anaerobic exercise, and understand the importance of recovery in different contexts.

So, what would next steps look like to address these knowledge gaps? Investigating recovery physiology can be done both in laboratory and field settings. For example, setting up a stream-side respirometry system (to avoid transporting fish, to use their native water source and to assess wild, field-acclimatized fish; Anlauf-Dunn et al. 2022), performing a chase protocol (Little et al. 2020) to elicit MMR, and subsequently measure oxygen consumption over time can provide us with estimates of the duration and cost of recovery. Blood and tissue samples could be obtained at various time points during recovery (e.g., 0, 1, 6, 12, 24 hr) to quantify lactate, ion levels, energy depletion, pH, and enzyme activities (among other metrics). Doing so on fish acclimated to different temperatures, and at various life stages, could provide insights on the effects of temperatures on recovery processes, as well as inter life stage differences. Earlier efforts have performed similar respirometry experiments, but rarely assess EPOC, tissue level metrics related to recovery, or compare across life stages, particularly on wild fish in the field.

Determining and quantifying the risk factors for delayed mortality are additional knowledge gaps that could be addressed. This review has shown that several studies have assessed immediate or short-term mortality, but few have been able to quantify delayed mortality (Table 2). One glaring issue for these types of studies is that the monitoring period for recovery has likely been too brief to adequately study the phenomenon of delayed mortality; most have been less than

Table 2. A sampling of both immediate and delayed mortality estimates in Pacific salmon following various forms of exhaustive exercise.

Species	Location	Type of exercise	Mortality	Reference
Gates creek sockeye salmon	Seton River Dam, British Columbia, Canada	Dam passage	Females: 56–60% Males: 29–31%	Roscoe et al. (2011), Burnett et al. (2014b)
Late-run Fraser River sockeye	Lower Fraser, British Columbia, Canada	High temperature	Late September: <10% Late August–early September: >90%	Cooke and Hinch (2005)
Chum salmon	Coastal British Columbia, Canada	Purse seine fishery (bycatch)	3.6–10.9%	Cook et al. (2018a)
Coho salmon	Strait of Juan de Fuca, British Columbia, Canada	Purse seine fishery (bycatch)	36.1%	Cook et al. (2018b)
Summer-run sockeye salmon	Fraser River (main stem), British Columbia, Canada	Catch-and-release fishery (including air exposure)	Handled only: 45% Captured: 64% Captured and air-exposed: 67%	Gale et al. (2011)
Harrison sockeye salmon	Harrison River, British Columbia, Canada	Catch-and-release fishery (including air exposure) and high temperatures	13 °C: 7% 13 °C + capture-release: 36% 13 °C + capture-release + air-exposed: 9% 16 °C: 30% 16 °C + capture-release: 0% 16 °C + capture-release + air-exposed: 30% 19 °C: 33% 19 °C + capture-release: 40% 19 °C + capture-release + air-exposed: 40%	Gale et al. (2014)
Hatchery-reared sockeye salmon	Nanaimo, British Columbia, Canada	15 min of high intensity chase	25%	Black (1957b)
Chinook salmon	Cape Fairweather, Alaska, USA	Trolling fishery	40–86%	Parker et al. (1959)
Sockeye salmon (adults)	Fraser River (main stem), British Columbia, Canada	Catch-and-release fishery (including air exposure), high temperatures and assisted (or not) ventilation	16 °C females, control: 37% 16 °C ventilated females: 100% 16 °C non-ventilated females: 75% 16 °C males, control: 20% 16 °C ventilated males: 30% 16 °C non-ventilated males: 10% 21 °C (regardless of treatment): 100%	Robinson et al. (2013)

24 hr, and many still have been less than 12 hr, so delayed mortality has likely been underestimated. One way to address this could be to tag fish with accelerometer tags (calibrated to estimate oxygen consumption, or to know what acceleration corresponds to aerobic vs. anaerobic swimming; Wilson et al. 2013, 2022), quantify anaerobic exercise, and subsequently evaluate mortality by tracking fish through the system. For example, linking the amount and duration of burst swimming by adult salmon at Hell's Gate in the Fraser River (or fish ladders, as in Burnett et al. 2014b) to subsequent survival along their migration to spawning grounds could shed light on the delayed consequences of anaerobic exercise. Perhaps, a fish that relies more heavily on anaerobic exercise is more likely to die en route to spawning. This approach would not get to the mechanisms of recovery but could be useful to assess anaerobic exercise and its consequences in wild fish. Many younger life stages are too small for similar studies, but small accelerometer tags do exist for smolt sized fish. A similar approach could also work to assess delayed mortality from angling. For example, an angled fish could be immediately placed in a respirometer to measure oxygen consumption for 1 to 2 hr, then tagged and released. How much the fish recovered within the first 1 to 2 hr post-angling could be linked to its behavior and subsequent survival, in the wild.

Recovery physiology and the physiological processes associated with delayed mortality are important in many aspects of fish research, including migration and angling (as described in the previous paragraphs), but also for discards from fisheries and aquaculture practices (Zhang et al. 2016; Hvas et al. 2020b; Warren-Myers et al. 2021), where fish tend to be crowded and acutely stressed during transportation and while undergoing various health treatments. Fish farmers have reported delayed mortalities following operations, and the physiological mechanisms involved here are likely similar. So, determining the mechanisms of recovery and the factors that affect these processes is key to many aspects of fish research, fisheries, conservation and management. Several examples of how current knowledge gaps could be addressed have been provided in this review, but there are many more ways in which this could be done. The authors call upon the research community for greater focus on recovery physiology and the consequences of anaerobic exercise in fishes.

7. Conclusions

The inability to successfully recover from exhaustive exercise (e.g. *via* high intensity rapids, high temperatures, fisheries interactions, etc.) can be a major contributor of mortality in adult Pacific salmon. Unsuccessful migration to spawning grounds results in zero lifetime fitness, with potentially devastating impacts for already threatened populations. With many populations already endangered or at-risk, issues pertaining to the failure to recover could become exacerbated, especially if salmon are faced with new challenges. In the Fall of 2018, more than 85,000 cubic meters of rock sheared off a 125 m high cliff and fell into the river along the Fraser River canyon (British Columbia, Canada), creating the so-called Big Bar Landslide. The landslide created a 5 m overfall, resulting in flows that were impassable for a large portion of the salmon migration season, trapping and killing migrating salmon below the slide until flow levels declined. For individuals that do pass, these high flows were energetically costly, with power requirements that certainly exceed their maximum aerobic capacities, and may result in delayed mortality due to recovery failure, as was previously shown for dam passage (Burnett et al. 2014b). The effects of the Big Bar Landslide and other hydraulically challenging stretches will only be aggravated with rapid warming of rivers; energetic demands will continue to rise but scope will continue to decline, making recovery more difficult (Farrell et al. 2008; Eliason et al. 2011, 2013a, 2013b; Martin et al. 2015).

Wood et al.'s classic paper in 1983 sought to understand why fish die after severe exercise, and suggested that the intracellular acidosis resulting from anaerobic biochemical pathways caused death. Despite great advances in this realm, there remains much to explore (Holder et al. 2022). This review demonstrates when and why recovery is important, and how failure to recover can be a large cause of mortality in Pacific salmonids that is likely to increase with the warming environment. Although this review focused on Pacific salmon here, the conclusions drawn are no doubt applicable to a wide range of fish species given that the need for recovery exists among all of them.

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