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Review

A review of adult salmon maximum swim performance

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Abstract

Salmonids undertake long and strenuous migrations that require aerobic endurance and anaerobic burst swimming. Anthropogenic activity and natural disasters can make already challenging migrations even more difficult. This reinvigorates a central question: *what is the maximum swimming capacity of adult salmon species across environmental conditions?* We synthesized literature on adult salmon swim performance (*Oncorhynchus* spp. and *Salmo salar*) to unfold what is known about how biological (sex and body size) and physical (temperature) factors affect swimming in adult salmon. Maximum anaerobic swimming—bursting, jumping, and leaping—are among the least studied swim performances in adult salmonids. Commonly, swim performance has been measured using swim flumes, but evidently adult salmon can swim faster in the wild than this set-up can capture. We show that larger fish can outswim smaller ones, and that thermal sensitivity of swimming differs inter-and -intra-specifically. Unresolved are how anaerobic swimming differs across temperatures, between males and females and across maturity states. This information can be used to inform exercise physiology research and future management and mitigation actions necessary to conserve these iconic, economically valuable species.

Key words: burst, U_{crit}, migration, aerobic swim, anaerobic swim

Introduction

Variation in fish swimming has strong implications for conservation, management, economics, and ecology, motivating countless studies across science disciplines (Palstra and Planas 2013; Hinch et al. 2022; Castro-Santos et al. 2022). For most fish, swimming is inherent to nearly all activities—fish swim to forage, avoid predation, catch prey, engage in social interactions, defend their territories, mate and reproduce, and migrate to new areas. All of these activities require some combination of bursting, burst-and-coasting, leaping, hovering, and steady sustained swimming, making these swimming modes paramount to the ecological and evolutionary success of fishes (Langerhans and Reznick 2010). Swimming performance can be described using a suite of metrics beyond swim speeds merging aspects of fish behaviour and motivation (Hinch et al. 2005), morphology, anatomy (Webb 2005), and fish physiology (Beamish 1978). In some fishes, such as salmonids, adults complete remarkably challenging migrations from the ocean back to their natal rivers to spawn (Brett 1965*b*; Thorpe 1988; Tamario et al. 2019). During the spawning migration, some adult salmon must overcome or avoid centerline encounter velocities above 4 m·s^{-1} for 10's of meters (Jackson 1950; Venditti et al. 2020), turbulent waters (Li et al. 2022), and ascend elevation gains over 1000 m (Crossin et al. 2004). Pacific salmon (*Oncorhynchus* spp.) undertake the challenging spawning migration only once in their lifetime (semelparity) and their success reaching the spawning grounds (and thus lifetime reproductive success) is determined by an individual's capacity for sustained and burst swimming (Brett 1965*b*; Burnett et al. 2014*a*).

Pacific salmon, *Oncorhynchus* spp. (Chinook, coho, chum, sockeye, and pink salmon), are an iconic genus that fulfill enduring cultural practices, provide numerous recreational fishing opportunities, support commercial economic fisheries, and provide food security across North Pacific rim (e.g., Atlas et al. 2021). Yet, many salmon populations in North America are increasingly being assessed as either threatened or endangered (Crozier et al. 2019; COSEWIC 2016, 2020, 2021). Several natural and anthropogenic factors are responsible for salmon becoming imperiled, including temperature rise, altered river flows, drought (Hinch et al. 2022; von Biela et al. 2022; Howard and von Biela 2023), habitat degradation, and fragmentation, including the presence of dams (Crozier et al. 2020; Belletti et al. 2020; Hinch et al. 2022). These environmental stressors can have profound negative effects on salmon migration and spawning success. An extreme example of an acute ecological change was the 2018 Big Bar Landslide that occurred at a remote section of the Fraser River (420 km upstream of on river mouth), the largest salmon-producing river in Canada. The upstream path to spawning grounds was entirely blocked by the fast water flows and turbulence at the Big Bar Landslide for extended periods in 2019 and 2020. Numerous populations of Chinook, sockeye, coho, and pink salmon were impacted, with over 10 of these pop-

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ulations already assessed as being threatened or endangered by the Committee on the Status of Endangered Wildlife in Canada, COSEWIC (COSEWIC 2016, 2020, 2021). This conservation disaster uncovered a pressing need to better understand the maximum swimming (bursting) capacity of adult migrating Pacific salmon across biotic factors (e.g., species, populations, sex, and body size) and across environmental conditions (e.g., temperature and flow).

Swim performance and energetics of fish have been studied extensively for decades producing a wealth of knowledge and numerous comprehensive reviews (Kieffer 2000; Plaut 2001; Liao 2007; Kieffer 2010; Holder et al. 2022; Jahn and Seebacher 2022). The primary objective of this review was to evaluate the literature on maximum swim speeds (through the water, not ground speeds) of adult salmonid species (Pacific salmon, *Oncorhynchus* spp., steelhead or rainbow trout, *O. mykiss*, or Atlantic salmon, *Salmo salar*) and discuss the results within the context of swimming physiology. We discuss sources of variation in swimming ability, identify major knowledge gaps in adult salmon swimming, and outline future research questions to address these gaps. The presented results may be used to develop management plans to predict passage success in any freshwater system (e.g., Bett et al. 2022) and to inform necessary mitigation plans to facilitate individual movement across barriers like dams, fishways, and natural hydraulic barriers (Birnie-Gauvin et al. 2019; Hinch et al. 2022; Cooke et al. 2022).

Swimming modes, energetics, and fatigue

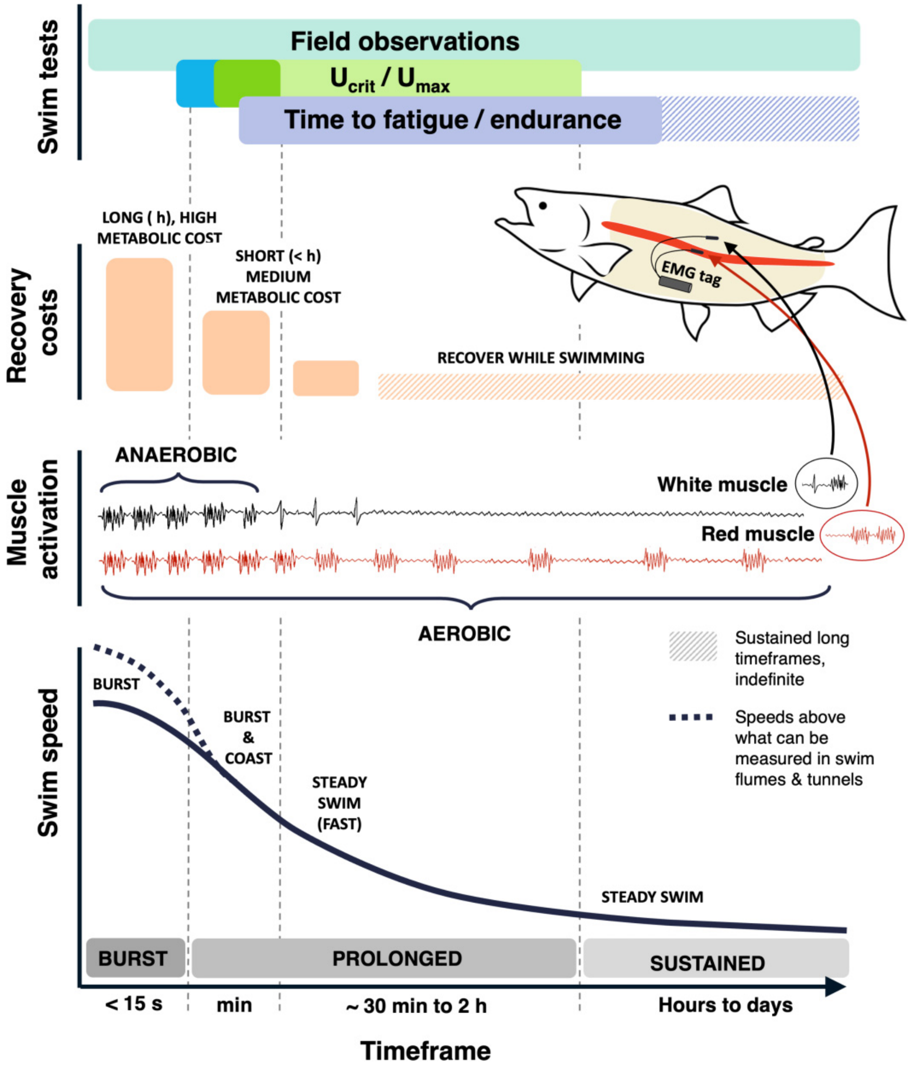
Fish swimming has been assessed in the context of exercise physiology (Eliason et al. 2013*a*; Eliason and Farrell 2016; Jahn and Seebacher 2022), locomotion kinematics and behaviour (Domenici 2010; Lea et al. 2016), hydrodynamics and robotics (Lauder 2015), and conservation and management (Rodgers et al. 2019; Bett et al. 2022; Cooke et al. 2020). Different swimming modes are driven first by extrinsic stimuli (e.g., water velocity, predation, temperature, light) with additional feedback by intrinsic factors such as fish's aerobic and recovery status (e.g., aerobic capacity and blood biochemistry). Fish use steady swimming for sustained daily behaviours, movement exploring new environments and paths, or hovering, and it does not lead to fatigue (Brett et al. 1958). Unsteady swimming consists of steady-sustained swimming interspersed with rapid bursts, turns, and consecutive burst-and-coast episodes (Castro-Santos 2005; Dutil et al. 2007), eventually leading to fatigue. However, sprinting, bursting, jumping, and predator escape responses are unsustainable, physiologically exhausting swimming modes that quickly lead to fatigue and more severe exhaustion (Black 1958; Kieffer 2000; Holder et al. 2022). Even though salmon migrations vary in difficulty (Crossin et al. 2004; Abe et al. 2019; Crozier et al. 2019), salmon engage in all of these swimming modes while maximizing their overall swimming efficiency *en route* to their spawning grounds (Beamish 1978; Jahn and Seebacher 2022; Wilson et al. 2022).

Steady-sustained swimming is predominantly powered by aerobic metabolism (via red muscle, composing only ~10% of total muscle mass, located along the lateral line in salmonids), keeping the energy supply and demand balanced (Nelson and Chabot 2011). Aerobic, red muscle fibers are small in diameter and highly capillarized, with high myoglobin, mitochondrial, and lipid content (Egginton and Sidell 1989; SäNger and Stoiber 2001). During aerobic swimming, the cardiovascular system can supply sufficient oxygen and substrates to the working muscle tissue, where energy (ATP) is generated via oxidative phosphorylation yielding ~36–38 ATP per one glucose molecule (Nelson and Chabot 2011). Likewise, the cardiovascular system can support the removal of by-products (mainly CO_2) generated by aerobic metabolism. Under optimal biotic and abiotic conditions across a range of lower velocities (~1 $BL \cdot s^{-1}$), salmonids can sustain aerobic swimming through the water almost indefinitely (Brett et al. 1958; Brett 1973) (Fig. 1), which makes this mode optimal and efficient for long migrations ensuring positive ground speed.

Fish begin bursting or combined burst-and-coasting under pressures from various extrinsic stimuli (e.g., current speed and predation) with secondary feedback from aerobic status (e.g., aerobic metabolism is insufficient to support swimming requirements; Weihs 1974; Marras et al. 2010). Burst swimming is powered by anaerobic metabolism (via white muscle, composing up to 85% of muscle mass in salmonids) (Geist et al. 2003; McKenzie 2011; Hachim et al. 2021). White muscle is largely anaerobic, composed of large muscle fibres with low capillarization, low myoglobin, lipid and mitochondrial content, but high glycogen concentrations (Egginton and Sidell 1989; SäNger and Stoiber 2001). A single continuous bursting event can only be maintained for <30 s (~15 s), though salmon can burst-and-coast at lower intensities from a few minutes up to 3 h (intermittent swimming mode with active and passive modes, see *Glossary*) (Bainbridge 1962; Beamish 1978; Bell 1991; Nelson and Claireaux 2005; Lauritzen et al. 2005; Castro-Santos et al. 2012) (Fig. 1). During anaerobic metabolism, ATP is produced rapidly without oxygen through glycolysis or phosphocreatine [PCr] metabolic pathways relying on finite endogenous substrates (glycogen, PCr). Although glycolysis is very rapid and thus can support high power output and faster swimming, it is unsustainable and yields only 2 ATP per glucose molecule, leading to a build-up of metabolic by-products that must be cleared to avoid muscle fatigue (Moyes and West 1995) and, thus, exhaustion. After bursting, fish must recover their endogenous reserves of glycogen, PCr, and free ATP, recycle built-up lactate back to glucose, re-establish blood ion and osmotic homeostasis, and raise blood pH (Scarabello et al. 1991; Milligan 1996; McDonald et al. 1998). Although streamlined fishes like salmonids are considered efficient at bursting and burst-and-coast swimming (Fish 2010), these modes are not energetically optimal for long migrations (Hinch and Rand 2000) (Brett 1967; Beamish 1978; Hvas and Oppedal 2017). Furthermore, if the physiological disturbance that underscores fatigue surpasses an individual's ability to recover, it can lead to post-exercise mortality (Black 1958; Wood et al. 1983; Burnett et al. 2014*a*; Brownscombe et al. 2017; Holder et al. 2022).

Migrating salmon use a combination of aerobic and anaerobic swimming (Hinch and Rand 2000; Lauritzen et al. 2010; Miyoshi et al. 2014; Bett et al. 2022) (Fig. 1). When fatigued, salmon must recover, which is aerobically costly and can last

Fig. 1. Conceptual presentation of applied physiology of swim performance and recovery. Conceptual timeframe representation of various processes during swimming in the field and well-established swim tests (U_{crit}, U_{max}, and endurance swimming tests). All sections—swim speed, muscle activation, recovery costs, and swim tests—are shown on the same conceptual timescale. The dashed lines that link all sections connect the processes with relative time based on swimming mode (burst, burst and coast, fast-steady swim, and steady sustained swimming). These modes are broadly grouped in bursting, mixed aerobic and anaerobic swimming with burst and coast (i.e., prolonged), and sustained swimming modes (bottom panel) (Beamish 1978). These modes alternatively can be identified by the amount of aerobic and anaerobic swimming, which describes the amount of white (anaerobic) and red (aerobic) muscle activation. In an experimental setting, this can be measured by electromyogram (EMG) tags. Anaerobic swimming leads to fatigue and requires recovery; the greater the anaerobic swimming effort, the higher post-swimming recovery costs a fish will incur. Fully aerobic swimming does not lead to fatigue, allowing fish to restore energy and clear metabolic waste products as it continues to swim aerobically. Therefore, the fastest swimming within the shortest timeframes necessitates the highest recovery costs. Most knowledge on fish swimming in salmon comes from field studies, laboratory studies using swim flumes (U_{crit} and U_{max}), or time to fatigue or endurance swim test using raceways, swim flumes, or similar apparatuses (top panel). In the wild, fish are required to swim at a broad spectrum of speeds. The U_{crit} and U_{max} swim tests are ramp-speed tests where the endpoint is when the fish can no longer continue to swim (reached fatigue). These tests can effectively measure steady swimming (aerobic; green), fast-steady swimming (aerobic and anaerobic; green), and burst-cost swimming capacities (highly anaerobic and aerobic, dark green = burst and coast, blue = sprint). However, fish cannot burst maximally (limited distance) or engage in any type of anaerobically powered leaping activity in swim flumes. The endurance swim tests measure sustained aerobic swimming, where fish occasionally may engage in unsteady swimming, but the chosen (constant) water velocity would not consistently require it. Endurance tests may or may not lead to fatigue. Numerous extrinsic and intrinsic factors affect swimming behaviour and swimming performance; some of these metrics are presented in the grey boxes. (icon credit: Bakunetsu Kaito, https://thenounproject.com/icon/salmon-1048779/).



many hours depending on the intensity of the exhaustive swimming and flow conditions during the recovery (Lee et al. 2003*a*; Milligan 1996; Wood 1991; Kieffer et al. 2011). The costly and long recoveries can delay migration (Caudill et al. 2007; Babin et al. 2021), increase susceptibility to predation, infection, and disease (Teffer et al. 2017, 2018), and accelerate depletion of finite energy stores in salmon (Rand et al. 2006). Even still, anaerobic swimming and recovery are required to migrate through river main stems and tributaries (e.g., Fraser River Canyon, Hell's Gate: (Hinch and Bratty 2000) to pass dams (Keefer et al. 2004, 2021; Caudill et al. 2007; Crozier et al. 2020; Hinch et al. 2022), to climb fishways (e.g., Castro-Santos 2005; Burnett et al. 2014*b*, 2014*a*, 2017), to pass culverts (Mueller et al. 2008), to jump across waterfalls (Kondratieff and Myrick 2006; Lennox et al. 2018*b*), and finally to spawn (Healey et al. 2003).

How is swim performance measured?

Fish swimming has been measured using different testing approaches and metrics. Here, "swimming performance" is defined considering a set of metrics including swimming velocity (the main quantitative focus), and physiological state and recovery (cardiorespiratory physiology, aerobic capacity, blood physiology, and recovery time). Numerous in-depth reviews discuss and compare the features, outcomes, and value of various fish swimming tests (DeLacy et al. 1956; Bainbridge and Brown 1958; Brett 1965*b*; Steffensen et al. 1984; Videler and Wardle 1991; Reidy et al. 1995; Hammer 1995; Jain et al. 1997; McDonald et al. 1998; Kieffer 2000; Plaut 2001; Nelson et al. 2002; Farrell 2008; Kieffer 2010; Ellerby and Herskin 2013; Tudorache et al. 2013; Kern et al. 2018; Hassan et al. 2022). Most swim performance studies, especially on salmonids, have been conducted in a controlled setting (field stations and laboratories) using swim tunnels (also known as swim flumes) and typically following standardized incremental velocity test protocols: critical swim speed test (U_{crit}; Brett 1964) and ramp-maximum swim speed test ($U_{\max}$, Farrell 2008; Tierney 2011; also called constant acceleration test U_{cat}, Oufiero et al. 2021; sprint test U_{sprint}, Starrs et al. 2011; or burst test U_{burst}, Reidy et al. 1995). Although using different durations, water velocity is increased during both U_{crit} and $U_{\max}$ tests until the fish can no longer maintain an upright position against the flow (see *Glossary*) (Brett 1964; Plaut 2001; Nelson et al. 2002; Farrell 2008; Starrs et al. 2011; Kern et al. 2018). Early studies in 1950s and 1960s used rotary tanks with accelerating current to examine swim speeds of fish (DeLacy et al. 1956, 1956; Paulik and DeLacy 1957*a*, 1957*b*, 1958). The experimental set-up of a rotary tank (round swim track: 3.35 m diameter, 30.48 cm wide outer channel swim area; Paulik and DeLacy 1958) and the swim test protocols (rotary-tank tank rotation speeds define water velocity in the swim channel; fish are introduced at a given flow from a holding box, or are subjected to increasing flows; exhaustion and/or fatigue are the endpoint of the test) are notably different than U_{crit} and $U_{\max}$ (see *Glossary*; Brett 1964). Long raceways, or flumes, for adult fish have been designed and utilized to measure maximum swim speeds in other fish species (50 m flume: smallmouth bass, *Micropterus dolomieu* [Peake 2004]; 20.5 m flume: a cyprinid species, *Schizothorax prenanti* [Li et al. 2022], and 25 m flume: Iberian barbel, *Luciobarbus bocagei* [Sanz-Ronda et al. 2015], and northern straightmouth nase, *Pseudochondrostoma duriense* [Sanz-Ronda et al. 2015; Sánchez-González et al. 2022]), but are not documented for use by adult salmon.

The U_{crit} and $U_{\max}$ tests allow investigators to understand mechanisms of swimming capacity, fatigue, exhaustion, and recovery (e.g., cardiorespiratory physiology, Eliason et al. 2011, 2013*a*, 2013*b*, 2013*c*; Clark et al. 2011; aerobic recovery: Lee et al. 2003*b*; Eliason et al. 2013*b*; Eliason and Farrell 2016; Hvas et al. 2021). However, U_{crit} and $U_{\max}$ predominantly examine aerobic swimming capacity. The maximum sprint (anaerobic) capacity cannot be measured in the tunnel (e.g., Farrell et al. 2003), because fish cannot gain positive ground speed, limiting acceleration and maximum burst ability. Notably, longer swim raceways can measure positive ground speeds that are twice as fast as U_{crit} (Peake 2004; see also Deslauries and Kieffer 2011). Often, swim tunnel size and design constraints prevent the fish from sprinting maximally with positive ground speeds (Peake 2004). Additionally, the calculated U_{crit} value depends on the velocity ramp protocol, size of the tunnel (e.g., affecting acceleration patterns of the fish) (Kern et al. 2018), and the behaviour of the fish in the tunnel (Peake and Farrell 2006). Therefore, U_{crit} is a test of individual swimming speed as well as behaviour and motivation. Despite these constraints, U_{crit} is one of the most widely used swim tests producing results useful in fisheries management (Bett et al. 2022).

Another way to measure swim performance is via fixed velocity tests (Paulik and DeLacy 1957*a*, 1957*b*, 1958; Brett 1967; Hvas and Oppedal 2017). These tests measure the time it takes a fish to fatigue at a fixed velocity. When this is performed across a range of velocities, the data produce time-to-fatigue (TTF, seconds to hours) *versus* swim speed curves (Paulik and DeLacy 1957*a*; Bainbridge 1962; Booth 1998). Time to fatigue swim speed relationships have been used to differentiate three swimming modes (sustained, prolonged, and burst) according to the classification by Beamish 1978 (e.g., Booth 1998; Castro-Santos 2005). Maximum effort bursting, however, can be extremely short, lasting < 5 s in several fish species (Bainbridge 1960, 1962). The short maximum performance may be used for jumping and leaping, which migrating adult salmon must do to overcome fast rapids (e.g., Hinch and Bratty 2000; Burnett et al. 2014*b*). Jumping and leaping speeds are among the least studied swim performances in adult salmonids (Powers and Orsborn 1985; Hammer 1995; Lauritzen et al. 2005, 2010; see Table 2 in Hammer 1995), an area that future studies may specifically address.

In the field, swim performance has been measured using telemetry and video recording. Swimming performance in wild migrating fish can be evaluated by their swimming speeds (cm), swimming duration at a given speed (min), distance covered (m, km), location (e.g., nearshore, depth), residence time in a given location (e.g., recovery, time it takes to transverse a given location; min, h), acceleration ($\mathrm{cm \cdot s^{-2}}$). In contrast to lab-collected data that are limited to measuring swim speeds ($\mathrm{cm \cdot s^{-1}}$, $\mathrm{cm \cdot s^{-2}}$) and recovery in confined space over a short term, field collected data provide more detailed information about maximum swimming capacity (speed) in the context of long-term swimming behaviour. Different types of tags have been particularly effective in measuring field swim performance in adult salmon (e.g., acoustic accelerometer tags: Wilson et al. 2013, 2022; Burnett et al. 2014*b*; Brownscombe et al. 2017; electromyogram (EMG) tags: Geist et al. 2000; Hinch et al. 2002; radio tags: Colavecchia et al. 1998; satellite tags: Hedger et al. 2017; ultrasonic tags: Stasko et al. 1976). Tagging studies provide information about salmon migration speeds, swimming patterns, and behaviour in the wild and in traversing fishways (Xie et al. 1997; Hinch et al. 2002; Cooke et al. 2013; Brownscombe et al. 2017; Matley et al. 2022; Wilson et al. 2022). However, tags must be calibrated in a laboratory setting to yield interpretable data on swim speeds, swim behaviour, and energy use (i.e., measure ground speeds and swim speed in low velocity environments; EMG tags: Rand and Hinch 1998; Thorstad et al. 2000; Geist et al. 2003; acoustic accelerometers: Wilson et al. 2013; Brownscombe et al. 2017). The calibrations are often done in swim tunnels (U_{crit} and $U_{\max}$ tests), which may limit the researcher's ability to obtain corresponding calibration values that match bursting speeds in wild migrating fish (Wilson et al. 2013; Cooke et al. 2016). Additionally, video tracking, more commonly used for enumeration, could also be used to measure field swimming performance (Hinch and Rand 2000; Standen et al. 2004), including jumping or leaping, in adult salmonids (Paulik and DeLacy 1957*a*; Lauritzen et al. 2010). Development, validation, and use of other types of tags, such as heart rate bio-loggers and high-resolution accelerometers, can help advance the understanding of swim performance, recovery, and behaviour of migrating and spawning fish in the wild (Prystay et al. 2017; Bjarnason et al. 2019; Meese and Lowe 2020; Zrini and Gamperl 2021; Twardek et al. 2021; Doherty et al. 2022).

Lastly, swimming in adult salmon has been evaluated on coarser time scales relevant to migrations (km·d^{-1}, km·h^{-1}, e.g., Bjornn and Peery 1992; Hanson et al. 2008*a*) but these times scales are not included in this review given the focus on anaerobic swimming. In other fish species or juvenile salmon, anaerobic swim performance has been evaluated using one-way sprint drag strips (Nelson et al. 2002; Haro et al. 2004) and fast-start escape response tests (juvenile Chinook salmon; Hale 1996). However, to our awareness, these techniques have not been used on adult salmon and thus are not included below.

Relative and absolute swim speeds

Fish swim performance is often expressed in speeds relative to an individual's body length (BL·s^{-1}) instead of in absolute swim velocity units (i.e., speed through the zero velocity water, cm·s^{-1}). Generally, larger fish can achieve greater absolute swim speeds but lower relative swim speeds (across species: Bainbridge and Brown 1958; Bainbridge 1960; in *O. nerka*: Brett and Glass 1973) (e.g., Fig. 2). For example, relative aerobic swimming generally scales with body size according to a negative log-linear relationship (meta-analysis: Katopodis and Gervais 2016; carp, *Cyprinus carpio,* and roach, *Rutilus rutilus*: Ohlberger et al. 2006), but relative anaerobic swimming may scale weakly or not at all with body size (log-linear functions, linear function, no scaling in cm·s^{-1}; across species: Goolish 1991; Ohlberger et al. 2006; Vogel 2008; Handelsman et al. 2010; Starrs et al. 2011; Oufiero et al. 2021). While using the relative swim performance (BL·s^{-1}) facilitates easy comparison of swimming capacity across species, the absolute swim speed (cm·s^{-1}) is required to understand the swim performance of an individual fish across ecologically relevant contexts.

When salmon approach rapids during their migration, each individual must swim upstream against similar range of encounter velocities (cm·s^{-1}) irrespective of their body length. Yet, fish tend to maintain steady aerobic swimming up to speeds of ∼1.5 BL·s^{-1} and then transition to anaerobic swimming modes at speeds of >2 BL·s^{-1} (steelhead and rainbow trout: Wilson and Egginton 1994; Chinook salmon: Geist et al. 2003; sockeye salmon: Eliason et al. 2013*b*; gilthead sea bream, *Sparus aurata*: Hachim et al. 2021; across species: Castro-Santos 2005, 2006) (Fig. 2). Consequently, the absolute velocity (cm·s^{-1}) at which a fish transitions to anaerobic swimming varies depending on its body size. For example, at a water velocity of 80 cm·s^{-1}, a 90 cm fish could still proceed upstream with positive ground speed while using aerobic swimming (net ground speed 55 cm·s^{-1}). However, at the same water velocity (80 cm·s^{-1}), a 30 cm fish would likely need to burst anaerobically at > 3 BL·s^{-1} speed to avoid negative ground speeds (Fig. 2) (e.g., Shi et al. 2022). The relative swim speeds are relevant to linking physiological and biomechanics to maximum performance, but the absolute swim speeds are useful when evaluating ecological outcomes (e.g., obstacle passage, predator avoidance) and allows a direct comparison across observations and species. Therefore, absolute swim speed is arguably the most relevant metric of swim performance in the context of natural conditions (e.g., the river flows).

Trends through time

Some of the first observations of adult salmon's maximum swim performance date back to early 1900s (e.g., Stringham 1924). Consistently, wild adult salmon have been observed to limit their swimming speeds to ∼250–300 cm·s^{-1} (Paulik and DeLacy 1957*a*; Powers and Orsborn 1985; Burnett et al. 2014*a*; Bett et al. 2022; Wilson et al. 2022), thus avoid swimming at their highest potential speeds. However, the first extensively studied adult salmon were from Great Central Lake and Somass River populations on Vancouver Island, British Columbia, Canada (Brett 1964, 1967) and steelhead trout, coho salmon, and sockeye salmom from Columbia River, Washington, Oregon, US, system (DeLacy et al. 1956; Paulik and DeLacy 1957*a*, 1958). The peak time in salmon swimming work was during the early 2000 s (40 studies between 2000 and 2010), but studies continue to be conducted in the field and laboratories (26 studies between 2011 and 2022) (Fig. 3). An increase in studies conducted on adult salmon can be partly attributed to the development of mobile field swim tunnel respirometers (Farrell et al. 2003) and advancements in tagging technology (e.g., use and calibration of EMG tags) (Geist et al. 2000; Hinch et al. 2002). In addition, telemetry

Fig. 2. Conceptual presentation of swimming physiology across size fish. The conceptual representation of metabolic requirements of different size fish (colours) swimming at increasing velocities, and aerobic and anaerobic metabolic power output of fish at different body sizes. In panels, (A) and (B) and oxygen consumption rate is plotted as a function of swim speeds, which is a proxy for the aerobic metabolism of fish. The dashed lines represent 2 BL·s^{-1} swim speed for all individuals (colour) in (A) and (B) panels. Oxygen consumption increases rapidly in fish of any body size until they reach $\sim$ 1.5 BL·s^{-1} speed (the grey band); then, the oxygen consumption begins plateauing slowly while the swim speed continues to increase. Individuals begin to swim anaerobically, burst-and-coast swimming around 1.5–2 BL·s^{-1} (A). Eventually, oxygen consumption tends to plateau, which indicates that the individual increasingly relies more on anaerobic swimming while reaching the maximum burst-and-coast or full burst swim speeds. The same relationships and physiological states are represented in panel (B) but in absolute swim speed (cm·s^{-1}). References literature: [1]Geist et al. (2003) and [2]Hachim et al. (2021).

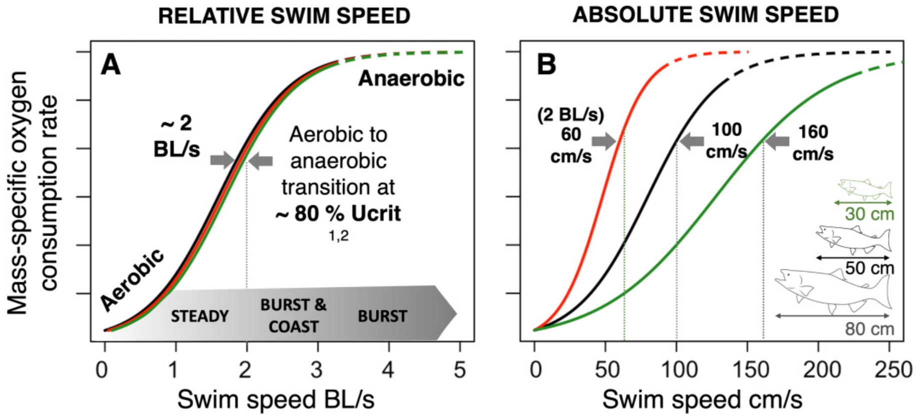
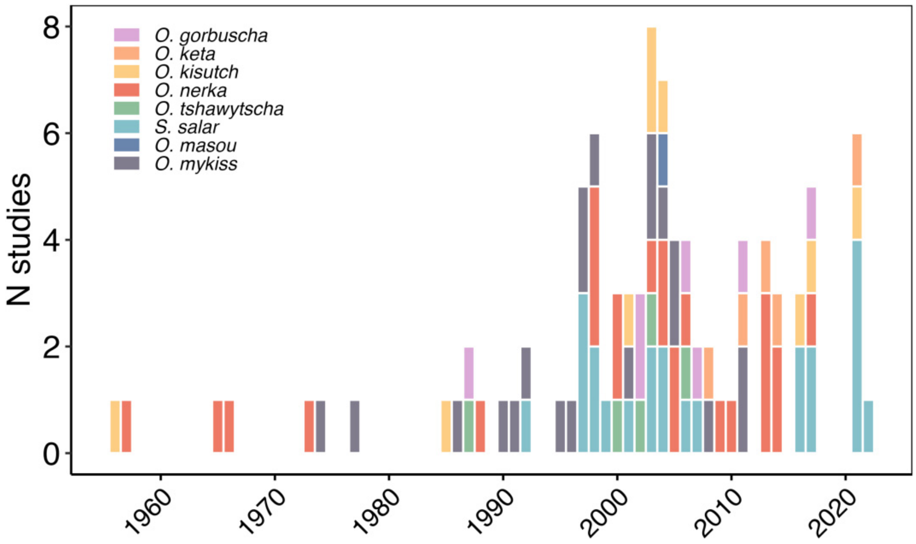


Fig. 3. Histogram of published studies reporting swim speeds in adult salmonids. Colour is for different species. Data were queried between 1950 and 2022.



continues to advance, providing promising opportunities to measure fine-scale field swimming speeds in migrating fish (Matley et al. 2022).

Methods

To consolidate and summarize the maximum swimming capacity of adult salmon, we performed a comprehensive review using Google Scholar and cross-references, and Web of Science and curated a dataset that compiles the maximum reported swim speeds of adult salmonids, their biological information, and biotic and abiotic conditions when available (Tables A1 and A2). Detailed methods are available in Appendix A.

Studies included (N = 103 studies, N = 3523 datapoints; Table A3, Appendix B) met the following criteria: (i) quantitative swimming speed of fish (groups or individuals) were reported either in text, table, plotted, or were personally provided by the authors, (ii) the included species were either, Pacific salmon, rainbow or steelhead trout, or Atlantic salmon, and (iii) all fish had reached adult life stage (Pacific salmon > 800 g; rainbow or steelhead trout > 500 g; Atlantic salmon > 500 g; or fish > 30 cm when mass was not reported). Each study was individually reviewed to extract species, swim speed (absolute or relative units; $\mathrm{ft\cdot s^{-1}}$, $\mathrm{cm\cdot s^{-1}}$, $\mathrm{m\cdot s^{-1}}$, $\mathrm{BL\cdot s^{-1}}$), fish size (g, kg, length), temperature, and sample size of the swum fish when available. Plotted swim speed values were extracted using tracking software ImageJ v 1.52 (Schneider et al. 2012). We extracted additional variables that can impact swim performance: type of swim test used (Table A4), extrinsic environmental conditions (Table A5), intrinsic physiological conditions of the fish (Table A6), sex, surgery or tagging procedures (Table A7), salinity, maturity levels, gonad size, water flow, discharge, reported occurrence of mortality, the origin of the fish (e.g., population, collection site, farmed), and the type of recovery performance evaluated in the original study, if any.

Our goal was to primarily focus on absolute swim speeds ($\mathrm{cm\cdot s^{-1}}$) as it most directly applies across ecologically relevant contexts. We calculated the absolute swim speeds ($\mathrm{cm\cdot s^{-1}}$) of fish from reported speed ($\mathrm{BL\cdot s^{-1}}$), and body length (cm) measures where possible, accepting the consequential uncertainty of these estimates (Appendix A; Supplementary Fig. S1). And lastly, throughout this review, we refer to two speed thresholds: (i) 2 $\mathrm{BL\cdot s^{-1}}$ because fish are generally required to rely on anaerobic swimming at this speed (Geist et al. 2003; Svendsen et al. 2010; Hachim et al. 2021), (ii) 250 $\mathrm{cm\cdot s^{-1}}$, because if salmon encounter these fast flows in the wild, they will avoid if possible, or need to burst to pass (Li et al. 2021; Bett et al. 2022).

In the sections below, we refer to (i) lab-measured swim speeds, which specifically include U_{crit}, U_{max}, one lab study on jumping, and unique studies using rotary or straight swim tracks, and (ii) field-measured swim speeds, which include speeds from tagged and tracked salmon, salmon examined in fishways, and swim speeds obtained using video analysis (Supplementary Table S1).

How fast can adult salmon swim?

The *maximum anaerobic* swim speeds of adult salmon remain largely unknown. Most ($N = 71$ out of 103) studies on adult salmon used U_{crit} or U_{max}, a predominantly *aerobic* swimming test with burst and coast *anaerobic* component generally reporting speeds below 250 $\mathrm{cm\cdot s^{-1}}$ and 4 $\mathrm{BL\cdot s^{-1}}$ (Figs. 4 and 5; Table 1). Specifically, swim performance using U_{crit} and U_{max} tests has been measured in 8 species across a broad temperature range (3.00–28.16 °C) and fish size (27.80–95.20 cm, body length) yielding 1263 measurements. Across species, these types of tests consistently yielded a maximum swim speed between 36.04 and 234.74 $\mathrm{cm\cdot s^{-1}}$ (mean: 115.15 $\mathrm{cm\cdot s^{-1}}$) or maximum relative swim speeds of ~2 $\mathrm{BL\cdot s^{-1}}$ (mean: 2.26 $\mathrm{BL\cdot s^{-1}}$, range: 0.64–4.25 $\mathrm{BL\cdot s^{-1}}$). The jumping velocities measured in the lab found a mean of 328.00 $\mathrm{cm\cdot s^{-1}}$, with max velocities of 546.00 $\mathrm{cm\cdot s^{-1}}$ in sockeye salmon (Lauritzen et al. 2005, 2010). These lab tests have yielded valuable information as salmon are likely to prioritize aerobic swimming over costly anaerobic swimming whenever possible, though a successful migration often requires burst swimming which remains to be fully elucidated.

Field studies, including fish at fishways, have measured adult salmon bursting at speeds up to ~400–800 $\mathrm{cm\cdot s^{-1}}$ (max speeds: 749.26 $\mathrm{cm\cdot s^{-1}}$ sockeye salmon, 481.58 $\mathrm{cm\cdot s^{-1}}$ Chinook salmon, 569.98 $\mathrm{cm\cdot s^{-1}}$ rainbow or steelhead trout, 350.52 $\mathrm{cm\cdot s^{-1}}$ coho salmon) and 6–13 $\mathrm{BL\cdot s^{-1}}$ (max speeds: 13.48 $\mathrm{BL\cdot s^{-1}}$ sockeye salmon, 6.60 $\mathrm{BL\cdot s^{-1}}$ masu salmon, 7.91 $\mathrm{BL\cdot s^{-1}}$ Atlantic salmon), which is much faster than measured in the lab (e.g., Fig. 4). Notably, the distribution of measured swim speeds is positively skewed (few fast swim speeds, many slow swim speeds; Fig. 4). It could reflect the balanced use of aerobic *versus* anaerobic swimming (Hinch and Bratty 2000; Wilson et al. 2022), but it also shows that well-described quantitative measures of maximum burst capacity (speeds, duration, frequency) of adult salmon are sparse (DeLacy et al. 1956; Paulik and DeLacy 1957*a*, 1958; Bell 1991; Booth 1998; Hinch and Bratty 2000; Reiser et al. 2011; Burnett et al. 2014*a*). The species-specific fastest reported swim speeds from lab and field studies are outlined in Fig. 4 and Table 1. However, these are likely underestimates of the maximal swim speed capacity of adult salmon.

Inter- and Intra-specific differences in swimming

Aerobic and anaerobic swimming ability in fishes varies between species (meta-analyses: Katopodis and Gervais 2016; Cano-Barbacil et al. 2020), populations (Atlantic salmon: Peake et al. 1997; sockeye and coho salmon: Lee et al. 2003*b*; sockeye salmon: Lee et al. 2003*b*; Eliason et al. 2013*b*, 2017; diverse species, non-salmonids: Jones et al. 1974, 2020; Billerbeck et al. 2001; Fu et al. 2014; Camarillo et al. 2020), individuals from the same population (pink salmon: MacNutt et al. 2006; Clark et al. 2011; Atlantic salmon: Anttila et al. 2014), and even temporally within individuals (pink salmon: Williams and Brett 1987; Atlantic salmon: Booth 1998). However, the database on adult salmon swimming was still data deficient to robustly estimate population-level differences in swimming ability (i.e., unknown origin of most fish). Therefore, the main focus here is devoted to the species-level swimming performance. It should be stressed that adult salmon from different populations have significantly different aerobic capacity and thermal performance (Lee et al. 2003*b*; Eliason et al. 2011; Van Wert et al. 2023) that in turn is directly linked with aerobic swimming performance but information on anaerobic performance differences among populations is still wanting.

The data coverage of swimming performance across species was uneven (Fig. 4). Sockeye salmon was the most studied of any Pacific salmon species (1971 data entries ($\mathrm{cm\cdot s^{-1}}$), 32 studies, 16 assigned populations). Their $\mathrm{U_{crit}}$ swim speeds (all populations together) were <200 $\mathrm{cm\cdot s^{-1}}$ (Fig. 5), which may relate to why sockeye salmon avoid flows ~ 240 $\mathrm{cm\cdot s^{-1}}$ (~ 4 $\mathrm{BL\cdot s^{-1}}$) in the field to prioritize aerobic swimming over costly anaerobic swimming (Li et al. 2021; Bett et al. 2022). However, swim capacity varies within a species (e.g., Fig. 6). Specifically, sockeye populations that face the most difficult migrations (river migration distance up to 1000 km, elevation gain above 1000 km, experience highest river dis-

Fig. 4. The swim speeds of adult salmon. (A) All compiled relative (greyscale) and absolute (colour scale) swim speeds in salmon (field measurements, U_{crit}, U_{max}, Jump, and alternative swim test results). (B) Species-specific relative and absolute (cm·s^{-1}) swim performance of salmon. The dashed lines are at 100 cm·s^{-1} (1/BL) aerobic swim speeds, 250 cm·s^{-1} (2.5/BL) anaerobic threshold (Bett et al. 2022; Geist et al. 2002), and 400 cm·s^{-1} (4 BL·s^{-1}), presumably anaerobic speeds. Species-specific maximum speeds and sample sizes in parentheses are provided on the panel.

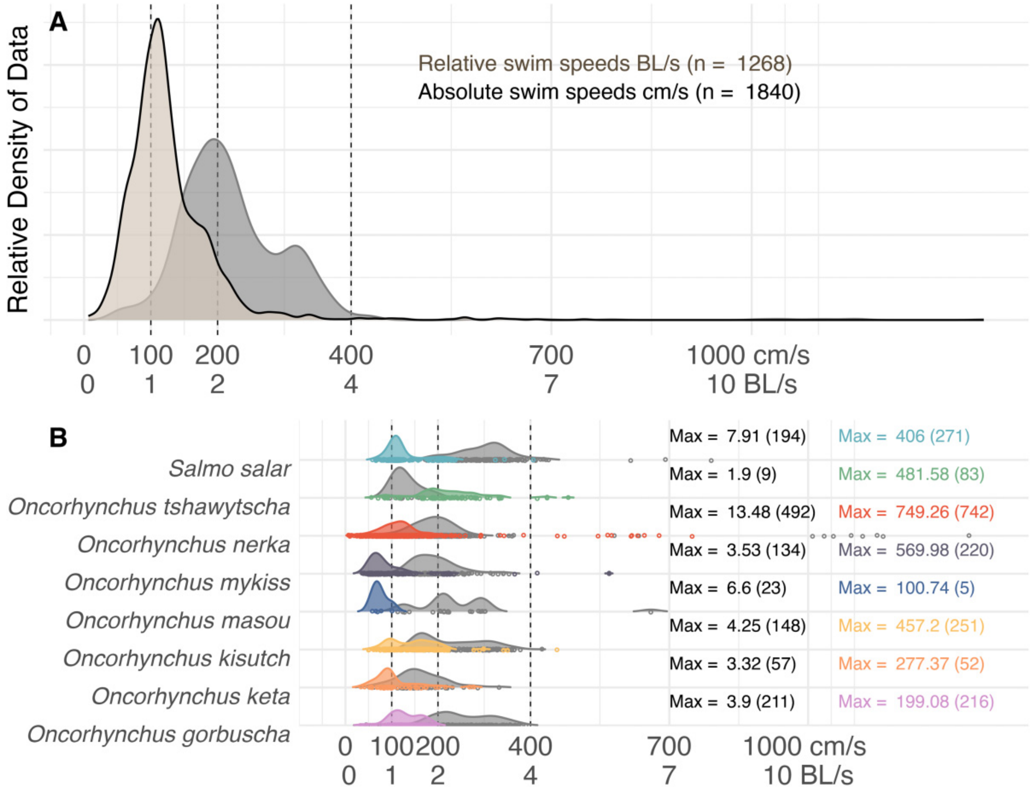
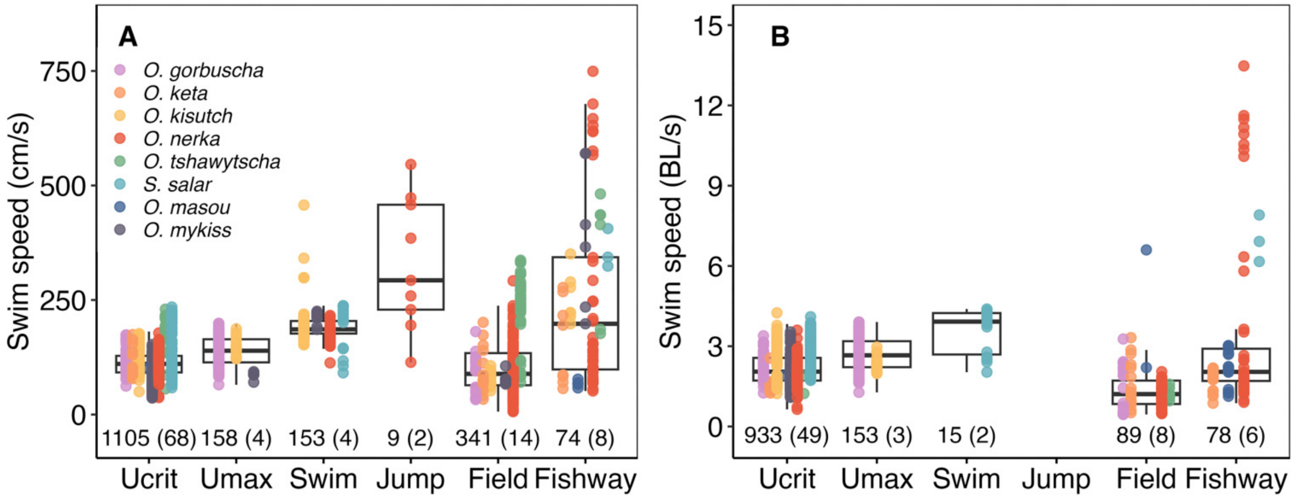


Fig. 5. Species-specific swim performance measured using different tests. Absolute swim speeds are in panel (A) and relative swim speeds are in (B). In both panels, the colour marks species, boxes cover the inner quartile range of data and whisker are outer quartile, the numbers indicate sample sizes: *n* datapoints (*n* studies). Repeat measurements are included (field test up to five highest speeds per individual, repeat U_{crit} tests).



charge rates leading to highest water velocities, > 4 m·s^{-1}) have up to 50% higher U$_{\mathrm{crit}}$ and more streamlined bodies compared to those with less demanding migrations (∼140 m·s^{-1} Early Stuart sockeye salmon, Lee et al. 2003*b*; Eliason et al. 2013*b*; and ∼90 cm·s^{-1} in Weaver Creek sockeye Lee et al. 2003*b*). Similarly, U$_{\mathrm{crit}}$ in brown trout, *Salmo trutta*, was higher in the upstream (fast-flow) population by ∼25% compared to downstream (slow-flow) populations (Jones et al. 2020). Pos-

Table 1. Summary on absolute speeds, body size metrics (length and mass), and temperature for each salmon species.

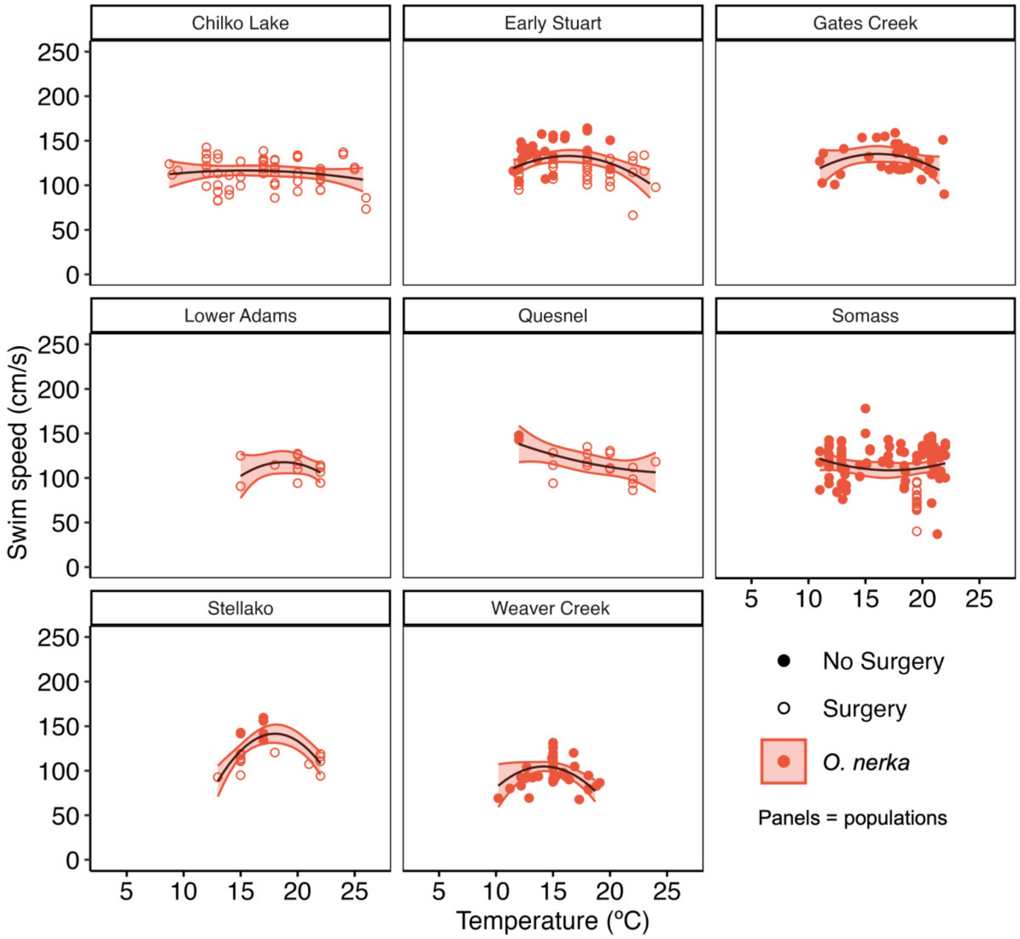
	Species							
	Sockeye salmon	Coho salmon	Chinook salmon	Chum salmon	Pink salmon	Masu salmon	Rainbow/steelhead trout	Atlantic salmon
Field								
Swim speed, cm·s^{-1}	92.51 (6.45–291.95)	74.85 (51.82–106.68)	234.15 (70.6–336.9)	90.56 (33.58–201.19)	93 (32.65–180.99)	–	76.81 (66.46–106.11)	–
N	231	18	50	20	24	–	14	–
BL, cm	59.12 (52.26–73.1)	–	77.6 (76–77.9)	61.8 (53.6–68.7)	59.24 (49.05–79.6)	–	39.5 (34.75–44.25)	–
BM, kg	1.99 (1.68–2.64)	–	5.92 (5.9–6)	2.03 (1.55–2.32)	2.65 (1.18–4.45)	–	–	–
T, °C	17.19 (9.5–19.35)	19.35 (19.35–19.35)	10.56 (10–13.5)	10.49 (9.45–12.3)	12.48 (9.45–14.65)	–	17.35	–
Fishway								
Swim speed, cm·s^{-1}	240.71 (51.42–749.26)	253.42 (198.12–350.52)	355.09 (176.78–481.58)	156.81 (56.77–277.37)	–	67.65 (58.14–77.21)	392.18 (198.12–569.98)	357.87 (323.9–406)
N	40	7	6	8	–	4	6	3
BL, cm	57.57 (52.76–61.31)	55.17 (35.56–61)	75.35 (50.8–96.52)	69.93 (62.05–76.2)	–	53.7 (51.45–55.95)	68.58 (60.96–81.28)	51.2
BM, kg	2.22 (1.8–2.8)	–	–	–	–	–	–	1.16
T, °C	17.3 (16.3–19.85)	19.03 (18.89–19.17)	19.17 (18.89–19.44)	–	–	–	19.21 (19.17–19.44)	10.1
Jump								
Swim speed, cm·s^{-1}	328 (114–546)	–	–	–	–	–	–	–
N	9	–	–	–	–	–	–	–
BL, cm	49.33 (29–59.5)	–	–	–	–	–	–	–
BM, kg	1.89 (0.28 –2.7)	–	–	–	–	–	–	–
T, °C	–	–	–	–	–	–	–	–
U_{crit}								
Swim speed, cm·s^{-1}	115.26 (37–178)	119.15 (50–176.76)	178.96 (55.97–230)	104.73 (78.29–174.61)	116.71 (62.23–173.93)	100.74	76.92 (36.04–152.83)	119.28 (58.48–234.74)
N	394	128	33	28	60	1	191	253
BL, cm	59.53 (41.8–69.5)	57.68 (49.8–71.4)	73.45 (45.5–95.2)	63.91 (59.55–71.79)	52.61 (46.1–55.5)	53.3	37.91 (30.1–51)	40.93 (27.8–63.8)
BM, kg	2.33 (0.75–3.56)	2.19 (1.36–4.11)	5.05 (1.31–11.5)	2.38 (1.9–2.86)	1.72 (1.36–1.82)	1.7	0.64 (0.44–1.47)	0.79 (0.25–2.54)
T, °C	16.87 (8.75–26)	10.92 (4.69–18.3)	13.3 (8–20)	12.77 (8–20)	14.17 (8.99–22)	12.75	9.64 (5–19)	12.2 (3–23)
U_{max}								
Swim speed, cm·s^{-1}	–	143.82 (121.85–187)	–	–	140.55 (65.07–199.08)	–	85.86 (70.6–93.6)	–
N	–	21	–	–	132	–	5	–
BL, cm	–	62.91 (60.6–66)	–	–	51	–	34.91	–
BM, kg	–	2.56	–	–	1.6	–	0.45	–
T, °C	–	13.14 (10–15)	–	–	17.56 (7.19–28.16)	–	9.76 (9.5–10)	–

Table 1. (*concluded*).

	Species							
	Sockeye salmon	Coho salmon	Chinook salmon	Chum salmon	Pink salmon	Masu salmon	Rainbow/steelhead trout	Atlantic salmon
TTF								
Swim speed, cm·s^{-1}	205.21 (65.2–286.51)	175.05 (91.44–304.8)	–	–	–	–	213.36 (121.92–304.8)	124.68 (60–240.46)
N	1229	158	–	–	–	–	98	147
BL, cm	41.74 (40.64–55.1)	60.68 (47.63–81.92)	–	–	–	–	65.34 (45.09–81.92)	46.51 (37.47–64)
BM, kg	0.91 (0.84 - 1.97)	–	–	–	–	–	–	0.99 (0.59 –3.16)
T, °C	17.52 (13–18.61)	10.94 (9.44–12.78)	–	–	–	–	10.97	10.9 (4.05–18)
Swim								
Swim speed, cm·s^{-1}	176.72 (112.78–216.41)	198.56 (152.4–457.2)	–	–	–	–	212.75 (185.93–225.55)	189.03 (91–237.57)
N	51	77	–	–	–	–	10	15
BL, cm	64.43 (54.61–75.57)	55.56 (26.04–76.2)	–	–	–	–	63.79 (58.74–67.95)	52.22 (40–59.58)
BM, kg	–	–	–	–	–	–	–	1.41 (0.85–1.76)
T, °C	14.52 (14.44–14.58)	10.05 (10–10.14)	–	–	–	–	7.08	12.41 (11.2–12.5)

Notes: Field is left empty when data were not available. *N*, sample size of swim speed values. TTF, time to fatigue. BM, body mass; BL, body length; T, mean temperature at the time of swimming. Values are provided as means (range), range was not available in all cases. The definitions of each swim test are provided in the Appendix A, Table A4.

Fig. 6. Population specific swim temperature performance curves of sockeye salmon tested in lab. The fitted lines are second order polynomials fit for each population separately. All models included fish length as a covariate, which is fixed at the mean value for each population; the shaded area shows the 95% confidence interval. The open circles are fish that had undergone surgery, which is known to decrease U_{crit} swim performance (Eliason et al. 2013*b*). Somass River Aggregate includes Grate Central Lake, Stamp River, Somass River populations of sockeye salmon. All regression equations are provided in Table 2.



sibly, swimming conditions and requirements earlier in life (juvenile stage, ocean migration) or migration could have a training effect on adult swimming performance contributing to inter-individual variation. Fish, including adult salmonids, can also exhibit training in the lab (Anttila et al. 2011). Pink salmon stood out for their high individual-level variation in swim speeds (Figs. 4 and 6; Standen et al. 2002; MacNutt et al. 2006; Clark et al. 2011), but also their relatively low (aerobic) swim speeds (133.10 cm·s^{-1} mean; 62.23–199.08 range, Fig. 4). This may be linked to the higher aerobic metabolic costs of swimming (and thus bursting) in pink salmon compared to other species (sockeye salmon: MacNutt et al. 2006), which partly could be explained by their drag-increasing body morphology (dorsal hump; Crossin et al. 2003) or by their small adult body size (smallest of all Pacific salmon species) requiring higher tail beat frequencies to achieve absolute swim speeds that are comparable to larger size species (MacNutt et al. 2006). Yet, pink salmon have an exceptional aerobic capacity (e.g., aerobic scope; Standen et al. 2002; MacNutt et al. 2006; Clark et al. 2011), they also behaviourally increase swimming efficiency by swimming in groups in shallower slower flowing sections near the shore of the river (Xie et al. 1997; Hinch et al. 2002) and by choosing a more "direct" routes (minimally exploring alternatives routes; Hinch et al. 2002) leading to lower total energy expenditure *en route* (e.g., Standen et al. 2002; Crossin et al. 2003). These examples demonstrate that salmonid swimming performance is complex—species and population-specific swimming behaviour (e.g., Standen et al. 2002; Hanson et al. 2008*a*; Wilson et al. 2014), biomechanical traits (e.g., body size, morphology and anatomy), and ecological conditions (e.g., temperature) all influence metabolic efficiency at any given swim speed (sockeye and coho salmon: Lee et al. 2003*b*; sockeye salmon: Eliason et al. 2013*b*; sockeye salmon parr: Eliason et al. 2017; review across species: Jahn and Seebacher 2022).

The distribution of species-specific swim speeds measured in the lab and field differ. One key reason for this trend is the inability to measure top burst speeds in the lab (discussed above). For example, Chinook, coho, sockeye salmon, and adult trout have been observed swimming or bursting at high ∼400 to 800 cm·s^{-1} in the field, but in the lab, their top speeds generally do not exceed ∼200 cm·s^{-1} (Fig. 5). However, in the field, it is clear that fish burst to traverse various types of fishways (Reiser et al. 2011), and natural rapids (review with case study: Bett et al. 2022; field tracking: Hinch and Bratty 2000) (Fig. 5). Additionally, wild fish can choose different paths prioritizing aerobic swimming over anaerobic, in some cases they behaviourally regulate swimming intensity (Xie et al. 1997; Hughes 2004), seek thermal refuge if required and available (e.g., Berman and Quinn 1991), and avoid predation (Quinn and Kinnison 1999). Larger fish have more options as they can make upstream progress swimming aerobically against higher absolute velocities compared to smaller fish (Fig. 2; Weaver 1963). Moreover, they may use this advantage to swim in deeper faster sections of the river to avoid dissipating energy by creating surface waves and excess drag acceleration (Webb et al. 1991 p. 199; Hughes 2004), or avoid predators (Quinn and Kinnison 1999). Lastly, the lab studies must be intentionally designed to measure maximum swimming performance. For example, the U_{crit} and TTF test using different water velocities or other alternative tests can produce different outcomes that consequently may or may not be relatable to field observed swimming performance (e.g., McDonald et al. 1998). All of these factors can introduce individual specific variation in swimming response and behaviour, partly explaining why lab and field swim speeds differ.

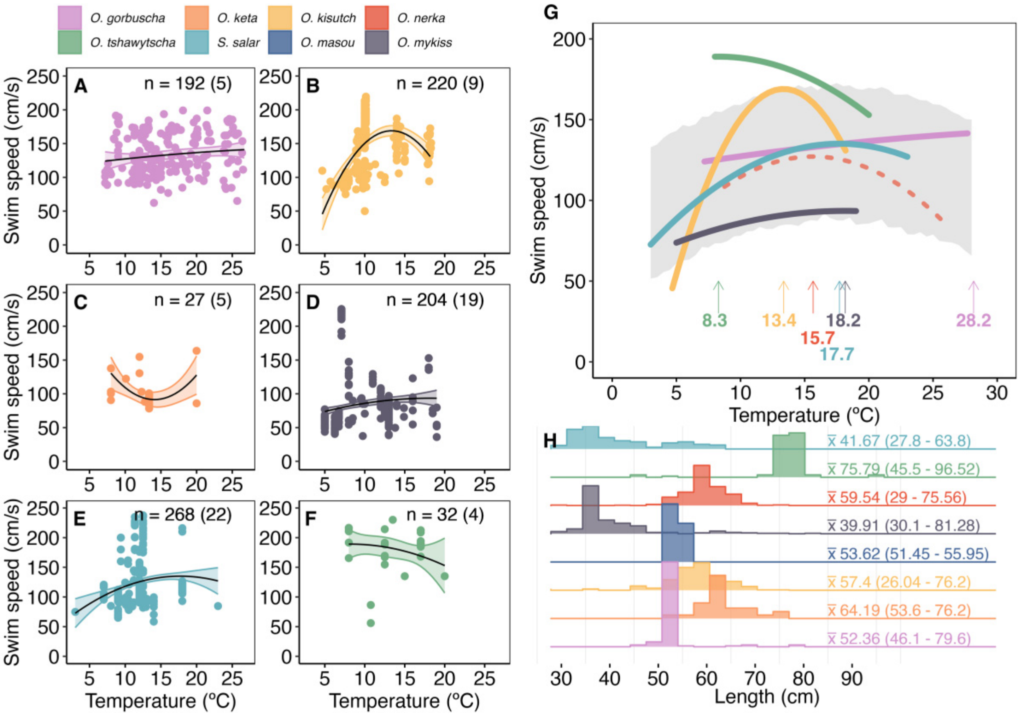
Temperature

Temperature is a master regulator of physiological processes in fish, and as such, it has a profound influence on swim performance (Brett 1971; Fry 1971). Thermal performance curves describe changes in physiological performance (e.g., U_{crit}, U_{max}) across temperatures and define where performance is optimal (T_{opt}, °C) (Brett 1971; Schulte et al. 2011). At temperatures above and below $T_{opt\text{-}SWIM,}$ swim performance may decrease, not change, or cease entirely, which can depend on the species, population, and recent thermal exposures (e.g., coho and sockeye salmon: Lee et al. 2003*b*; sockeye salmon: Eliason et al. 2013*a*; pink salmon: Clark et al. 2011; halted swimming in $> T_{opt\text{-}SWIM}$: Steinhausen et al. 2008). Studies examining physiological thermal performance in salmon are fairly abundant, but collective knowledge of swimming performance under different thermal regimes including swimming below $T_{opt\text{-}SWIM}$ is still fragmented (reviews: McCullough 1999; Richter and Kolmes 2005; Zillig et al. 2021). The thermal performance of burst swimming, specifically, is not characterized in adult salmon.

We aimed to describe how maximum swimming performance changes across temperatures at population levels (e.g., sockeye salmon, Fig. 6). However, we were only able to evaluate temperature dependence of lab-measured swim speeds at the population level for sockeye salmon ($N = 8$ populations; Fig. 6), while others were assessed at the species-level ($N > 30$ datapoints, 10 °C temperature range; data at a finer level were limited) (Fig. 7). The $T_{opt\text{-}SWIM}$ for different sockeye salmon populations largely differ in accordance with their historic exposures to different temperatures during migration (Eliason et al. 2011) (Fig. 6, Fig. S2). At species-level for coho salmon, we estimated a $T_{opt\text{-}SWIM}$ at 13.36 °C ($cm{\cdot}s^{-1}$) (Fig. 7D), which was markedly higher than the reported $T_{opt\text{-}SWIM}$ performance of Chehalis coho (8.50 °C, Lee et al. 2003*b*) but comparable to Chilliwack coho salmon (14.00 °C, Kraskura et al. 2021). Some of this variation in $T_{opt\text{-}SWIM}$ between populations and species could be associated with differences in cost of swimming that depends on temperature (Eliason et al. 2013*a*) and body morphology (e.g., species and populations with longer and more strenuous migrations have more slender bodies reducing swimming costs) (Crossin et al. 2004; Kinnison et al. 2003). The interactive effects of temperature and body morphology on cost of transport (COT) and thus maximum swimming performance in adult salmon have not been teased apart. Notably, Chehalis coho salmon swum at different temperatures (~7 and 11 °C) had diverging COT at U_{crit} speeds, where fish in warmer temperatures had lower COT (Lee et al. 2003*b*). Additionally, Eliason et al. (2013*a*) found no differences in COT at U_{crit} speeds between three sockeye salmon populations (Quensel, Early Stuart and Chilko) that were swum at their T_{opt}, and above and below T_{opt}; however, the COT would differ between populations without temperature-normalizing their performance.

Thermal performance curves for other species-level trends did not have a clear bell-shape (Fig. 7G), thus the $T_{opt\text{-}SWIM}$ values identified here have a high level of uncertainty and could be explained by various factors. Foremost, it may be due to the lack of population-level analysis, low samples sizes, or insufficient data across a broad temperature range. In addition, the temperature effects on swimming performance can also depend on the experimental details, such as swim protocols, surgery, temperature exposure (e.g., acclimation rates and durations), and the origin and maturation status of the fish. In the collated data, the duration of temperature acclimations before testing swim performance varied between acute (hours e.g., Clark et al. 2011), and short term (1–5 days e.g., Eliason et al. 2013*b*, Lee et al. 2003*b*, MacNutt et al. 2006). Possibly, the swim performance after acute temperature-exposure is underestimated compared to if fish were acclimated for longer, but short acclimations (~24 h) are ecologically relevant for salmon migrating through the thermally heterogenous river. Moreover, a study comparing the impact of acclimation period duration on swim performance in cutthroat trout found no difference in U_{crit} between fish acclimated for 48 h *vs.* 3 weeks to 7, 14, and 18 °C (MacNutt et al. 2004). In pink salmon swim speeds were nearly insensitive to temperature (no peak, $T_{opt\text{-}SWIM}$ ~28.00 °C; range 7.19–28.16 °C), but most data (61%; $N = 132/193$) are individual U_{max} speeds after an acute 4–10 h temperature change (Fig. 7A) (Clark et al. 2011). The U_{max} may not be directly comparable to U_{crit} performance, and swimming after acute temperature change could be different compared to that in longer-acclimated fish (e.g., ≥ 1-day acclimation). Additionally, swim performance of Atlantic salmon from the lab lacked a clear thermal performance curve and $T_{opt\text{-}SWIM}$ (Fig. 7E), which could be because most of these fish were farm-raised. Swim performance in adult Chinook and chum has been measured across a wide range of temperatures but has a low sample size adding uncertainty to our estimates (chum salmon: $N = 28$, Fig. 7C, Chinook salmon: $N = 33$, Fig. 7F; 8.00–20.00 °C both). Lastly, some observed variation could be attributed to differences in fish's maturity state. For example, a few studies have shown that swim performance in adult migrating

Fig. 7. Absolute swim speeds measured across species and temperatures, specifically in lab tests (U_{crit}, U_{max}, swim, and jump tests). (A–F) Species-specific data with fitted 2nd order polynomial fits (black line), and 95% confidence interval bounds (shaded); species that were swum across at least 10 °C are presented. The numbers indicate sample sizes: n datapoints (n studies). Species-specific thermal performance curves are shown together in (G) to facilitate interspecific comparison of estimated optimal ranges for swimming (arrows and $T_{\text{opt-SWIM}}$, °C). The shaded area is the 95% confidence interval area for the thermal performance curve estimated across all salmon species. The fit equation for each species is reported in Supplementary Material. Length was included as covariate in all fits and here is fixed at the mean value for species. Panel (H) shows the histogram of body lengths for each species; means ($\bar{x}$) and ranges (cm) are on the panel. All regression coefficients are provided in Table 2.



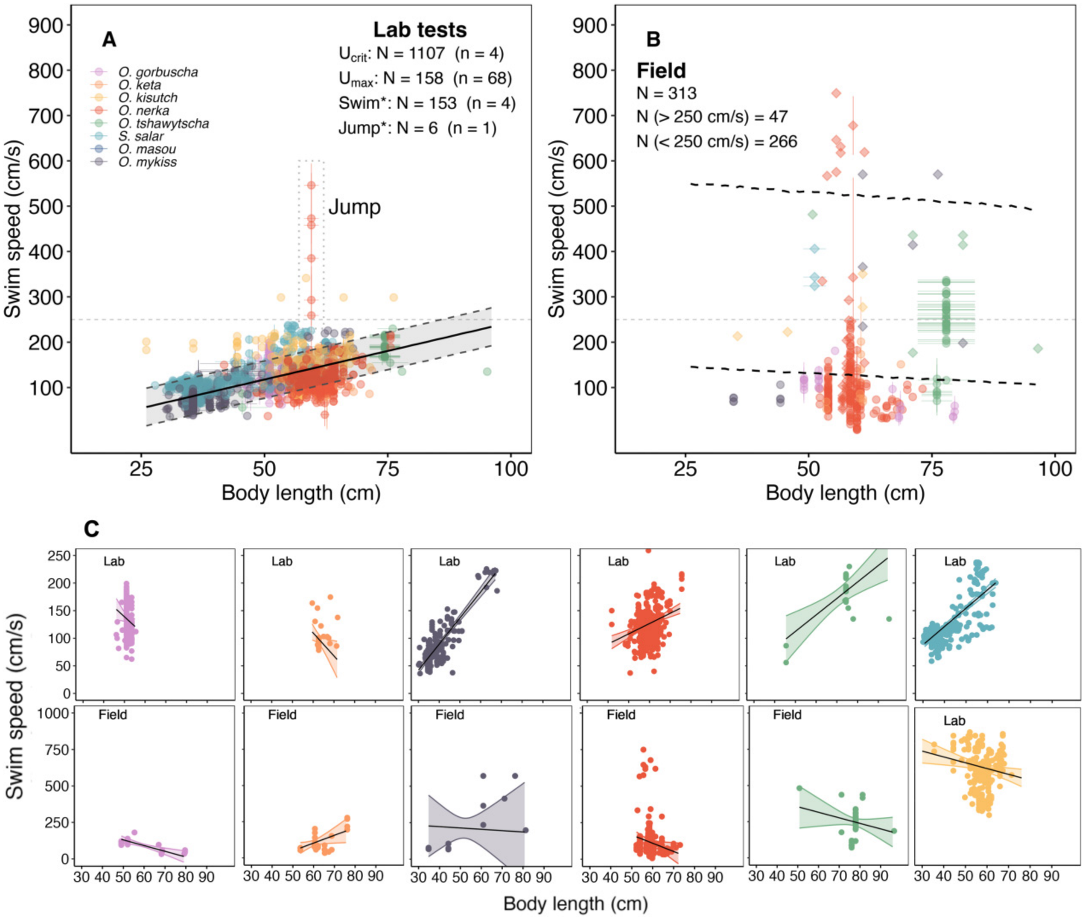
salmon can differ along the migration and thus maturity (Atlantic salmon: Booth 1998, pink salmon: Williams and Brett 1987; sockeye salmon: Paulik and DeLacy 1958), which may interact and overlap with broad-range temperature exposure. Some salmon populations may begin their migration at different maturity states (e.g., spring Chinook salmon from Klamath basin are less mature than fall Chinook; Hearsey and Kinziger 2015; summer (immature) and winter (mature) steelhead trout; Busby et al. 1996) providing an opportunity to compare how maturity states affect swimming performance. Clearly, the optimal temperatures for swimming, particularly at intra-specific levels need to be refined (Lee et al. 2003*b*, 2003*a*; Eliason et al. 2011; Zillig et al. 2021). To better reflect the modifying factors identified above, the $T_{\text{opt-SWIM}}$ may be better presented as a range of temperatures over which swimming is optimized (i.e., 80 or 90% of maximum) rather than a single value (Eliason et al. 2013*a*).

The temperature effects on anaerobic burst swimming have not been systematically examined in adult salmon and only sparsely studied among other fish species (Beddow et al. 1997; Guderley et al. 2001; O'Steen and Bennett 2003; Sylvestre et al. 2007; Muhawenimana et al. 2021). Burst performance can be insensitive to temperature (sauger, *Sander canaden*: Dockery et al. 2017*b*; opaleye, *Girella nigricans*: Hardison et al. 2021), can increase with temperature (juvenile European sea bass, *Dicentrarchus labrax*: Claireaux et al. 2007), or can decrease (juvenile sockeye salmon: Burt et al. 2012; Atlatic cod, *Gadus morhua*: Sylvestre et al. 2007). Adult salmon increase their reliance on anaerobic metabolism at higher temperatures (Brett 1964; Jain and Farrell 2003; Steinhausen et al. 2008; Eliason et al. 2013*a*; Abe et al. 2019), but the differences in bursting capacity (e.g., speed, distance, acceleration) across changing temperatures have not been quantified. Further, the higher bursting activity under warming could have higher negative consequences, namely post-exercise mortality (e.g., Holder et al. 2022). The thermal sensitivity of adult salmon anaerobic swimming remains a major knowledge gap.

Body size

Larger fish can generate greater thrust (Webb 1976) and swim faster (Fig. 2; Fig. 8) (across species: Bainbridge 1958; Brett 1965*a*; Brett and Glass 1973; Webb 1976; Goolish 1991; Hammer 1995; Booth et al. 1997*b*; McDonald et al. 1998; Mesa et al. 2008; Vogel 2008; Bellinger et al. 2014; Oldham et al. 2019; Jones et al. 2020; Cano-Barbacil et al. 2020). To robustly estimate the degree to which body size influences swimming,

Fig. 8. Body size influence swim speeds measured in the lab and field. (A) Positive relationship between swim speeds and body length in lab studies; the n datapoints (n studies) for each included swim tests are plotted in panel. (B) Field measured swim speeds above 250 $m \cdot s^{-1}$ were weakly positively associated with body length, and speeds < 250 $cm \cdot s^{-1}$ were weakly negatively associated with fish length; samples sizes on the panel. Regressions are mixed model estimated for adult salmon. Speeds > 250 $cm \cdot s^{-1}$ are assumed anaerobic speeds and are visually marked by dotted line. The error on datapoints is s.d. for groups of fish. (C) Species-specific relationships between body length and absolute swim speeds in adult salmon; the regressions are simple linear model predictions assuming mean measured temperature for each species subset; the shaded area is the 95% confidence interval area. All regression coefficients are provided in Table 2.



it is necessary to have a sufficient sample size across a broad body size range (ideally a ten-fold difference e.g., White and Kearney 2014). The adult salmonids included in this review were between ∼ 30 cm (*O. nerka*, *O. mykiss, S. salar*) and ∼ 80-90 cm, BL (*O. mykiss*, *O. gorbuscha, O. tshawytscha*) (Fig. 8). The best estimates of species-specific differences in fish length *versus* swim speed relationships are provided in Fig. 8C.

Body size scaling of field swim performance was weaker than scaling of lab-measured swim performance. Lab data indicated that larger adult salmon could swim significantly faster than smaller fish (speed increased by 2.53 ± 0.13 $cm \cdot s^{-1}$ for each cm FL, $N = 1385$, Chi-square $= 356.41$, df $= 1$, $p = 2.20E{-}16$; Table 2, Table S2, Table 2, Fig. 8A). In contrast, field-measured aerobic speeds (<250 $cm \cdot s^{-1}$) scaled negatively (slope $= -0.54 \pm 0.52$, $N = 266$, Chi-square $= 1.07$, df $= 1$, $p = 0.3$; Table 2, Table S2, Table 2, Fig. 8B). A similar, somewhat surprising, negative relationship was also observed in adult Atlantic salmon traversing a fishway in Norway (Lindberg et al. 2016). Differences between lab and field size scaling relationships may be driven by fish behaviour, choice, and physical environment (Castro-Santos 2005; Peake and Farrell 2006), or by differences in the testing approach (McDonald et al. 1998). For example, in the lab, the hydraulic conditions are carefully controlled, and fish are confined in swim tunnels swimming against near laminar flows. Furthermore, the selected swimming test can produce different scaling effects; specifically in juvenile salmonids the size effect was stronger using exhaustive TTF than modified U_{crit} (McDonald et al. 1998). In the field, including at fishways, flows are often turbulent, and fish can freely choose which path to travel, and which flows to avoid (Standen et al. 2004; Castro-Santos 2005; Lindberg et al. 2016; Bett et al. 2022). Turbulent flows could reduce fish swimming speed (U_{crit}: Tritico and Cotel 2010), have no measurable effect on swimming (TTF tests: Nikora et al. 2003), or be exploited by fishes (Liao 2004; Hinch and Rand 2000) (physiological, behavioural mechanisms are reviewed by Liao 2007). The effects of turbulence on swimming depends on the type of turbulence (intensity,

Table 2. Estimates and models of species-specific swim performance across temperatures and body size (body length, BL).

Description	N	β_0 (SE)	β_1 (SE)	β_2 (SE)	β_3 (SE)
Field	313	162.84 (228.4)	−10.99 (27.9)	0.6 (0.95)	0.91 (1.14)
Field (>250 cm·s^{-1})	47	−1174.52 (1059.23)	225.45 (150.09)*	−7.22 (5.17)*	−0.83 (2.34)
Field (<250 cm·s^{-1})	266	158.6 (35.96)	–	–	−0.54 (0.52)
Lab-collected data	1402	−62.27 (13.94)	6.36 (1)*	−0.18 (0.03)*	2.53 (0.13)*
Species-specific relationships: lab collected data only					
Pink salmon	193	291.88 (90.79)	1.45 (2.59)	−0.02 (0.07)	−3.44 (1.72)*
Chum salmon	28	565.71 (163.34)	−29.52 (9.39)*	1.05 (0.33)*	−4.16 (1.76)*
Coho salmon	226	−65.68 (39.71)	43.82 (5.55)*	−1.64 (0.22)*	−1.01 (0.37)*
Chinook salmon	33	−48.44 (108.28)	4.36 (12.86)	−0.26 (0.49)	2.99 (0.75)*
Rainbow/steelhead trout	206	−128.82 (11.66)	4.13 (1.99)*	−0.11 (0.09)*	4.73 (0.2)*
Atlantic salmon	273	−93.73 (20.62)	10.22 (3.29)*	−0.29 (0.12)*	3.33 (0.17)*
Sockeye salmon	461	−79.65 (33.35)	12.04 (3.57)*	−0.38 (0.1)*	1.88 (0.31)*
Sockeye salmon: population-specific relationships					
Chilko Lake	62 (62)	76.3 (49.08)	2.91 (3.58)	−0.09 (0.1)	0.3 (0.68)
Early Stuart	64 (34)	36.74 (73.47)	19.64 (6.75)*	−0.6 (0.2)*	−1.07 (1.08)
Gates Creek	36	−435.84 (846.33)	19.95 (12.06)	−0.62 (0.36)	6.42 (14.17)
Quesnel	48 (12)	225.03 (105.46)	−8.07 (10.39)	0.15 (0.29)	−0.2 (1.02)
Somass Aggr.	121 (16)	171.05 (80.02)	−11.59 (9.29)	0.34 (0.28)	0.65 (0.55)
Weaver Creek	40	211.74 (221.05)	38.42 (13.16)*	−1.35 (0.42)*	−6.11 (2.35)*
Lower Adams	12 (12)	−127.44 (263.34)	28.32 (37.18)	−0.76 (0.97)	−0.31 (3.47)
Stellako	19 (13)	−578.56 (199.55)	75.33 (20.53)*	−2.09 (0.56)*	0.67 (1.07)

Significant factor, statistics can be found in the Supplementary Table S2.

"Somass Aggr." represents Somass River Aggregate: Grate Central Lake, Stamp River, Somass River populations of sockeye salmon. The equation for each relationship is: Swim speed $\sim \beta_0 + \beta_1 T + \beta_2 T^2 + \beta_3 BL + error$. *T, temperature (° C); BL, body length (cm). For population-specific trends, the sample size of fish that had undergone surgery is indicated in parentheses. Confidence intervals, the statistics of random effects, and the overall fit metrics of the field and lab swim speed models are available in the supplement.*

periodicity, orientation, scale; Lacey et al. 2012) as well as the size of the fish (i.e., fish to vortex size ratios). If the turbulent conditions are not beneficial, fish will behaviourally avoid it by searching alternative ways or bursting through turbulent sections to limit transit time (Odeh et al. 2002; Li et al. 2022) avoiding high costs of swimming through turbulence (Hinch and Rand 1998; Enders et al. 2003). Further, large fish could also prioritize exploring alternate paths avoiding fast flows because it is cumulatively more energy-efficient, not because of their inability to swim fast (Lindberg et al. 2016, but see Standen et al. 2004) or limited anaerobic exercise potential (Casselberry et al. 2023). Lastly, the scaling of the field-measured anaerobic (>250 m·s−1) was weakly negative but not reliable due to low sample size (slope $= -0.83 \pm 2.34$, $N = 63$, Chi-square $= 0.12$, df $= 1$, $p = 0.72$), while the overall field reported field speeds scaled weakly positively (slope $= 0.91 \pm 1.14$, $N = 313$, Chi-square $= 0.6461$, df $= 1$, $p = 0.42$) (Table 2 and supplementary Table S2; power analysis with recommendations for more robust scaling relationships is provided in Supplementary Fig. S3). The behavioural components of swimming may be particularly important to make ecologically relevant predictions about swim performance across different size adult salmon.

The relationship between individual swim speeds and body size can be nonlinear, which could be partly explained by nonlinear mass-specific tissue-level physiology. Accordingly, mass-specific glycolytic (anaerobic) enzyme activity (lactate dehydrogenase and pyruvate kinase) scaled positively and nonlinearly following a power function in white muscle in various fishes (Childress and Somero 1990; Norton et al. 2000; Patterson et al. 2004*a*). Additionally, metabolic fuel storage that powers anaerobic swimming scaled positively, but linearly with size in salmonids (i.e., endogenous ATP and glycogen g^{-1} in rainbow trout: Ferguson et al. 1993; fat, endogenous ATP, glycogen stores, and somatic energy in Atlantic salmon*:* Lennox et al. 2018*a*). Worth noting, the mass-scaling of these tissue-level physiological processes is species-specific and non-uniform across tissue types (Childress and Somero 1990; Goolish 1991; Norton et al. 2000; Norin and Malte 2012). More physiology-informed mechanistic studies (Cooke et al. 2020; Eliason et al. 2022), particularly on wild adult salmon, are required to better understand the scaling of swimming performance and field swimming behaviours.

It must be acknowledged that the average body size of returning adult salmon is declining, which adds an additional economic and ecological concern (Oke et al. 2020; Ohlberger et al. 2023). Changing population size distribution towards smaller body size can remove the advantages that larger individuals possess, including their ability to swim faster, capacity to choose alternate paths while relying on aerobic swimming, higher energy storage, and higher fecundity (Barneche et al. 2018). It is clear that body size is a fundamental morphometric that is important not only for swimming performance, but also for species' ecological success and economic value (Oke et al. 2020).

Sex

Female and male migrating adult salmon invest most of their finite energy stores towards swimming, recovering, and reproduction (Fleming 1996; Hinch et al. 2021). However, the energetic costs of reproduction in migrating salmon (gonad development and maintenance) are disproportionally higher in females compared to males (Patterson et al. 2004*b*), which could lead to sex-specific differences in their swim performance (reviewed by Fenkes et al. 2016). Numerous studies have addressed sex-specific swim performance in fish, with a few on adult salmon (Williams and Brett 1987; Standen et al. 2002; Farrell et al. 2003; Steinhausen et al. 2008; Roscoe et al. 2011; Clark et al. 2011; Wilson et al. 2013; Eliason et al. 2013*b*; Burnett et al. 2014*b*; Makiguchi et al. 2017; Kraskura et al. 2021; non-salmonid species: Nelson 1989; Reidy et al. 1995; Plaut 2002; Cooke 2004; Ghalambor et al. 2004; Mateus et al. 2008; Svendsen et al. 2009; Belk and Tuckfield 2010; Hockley et al. 2014; Conradsen and McGuigan 2015; Srean et al. 2017). Most of these studies focus on reproductively active, mature fish (e.g., Kraskura et al. 2021), or sexually dimorphic species (non-salmonid species: Oufiero et al. 2014; Conradsen and McGuigan 2015). Only a few studies have compared swim performance in males and females across temporal scales, such as reproductive seasons (non-salmonids: Nelson 1989; Cooke 2004) and at different maturity states (Williams and Brett 1987; Booth et al. 1997*a*; Svendsen et al. 2009).

Swim performance differences between male and female adult salmon tested in the lab remains inconclusive. For example, U_{crit} was lower by ~0.3 $\mathrm{BL}\cdot\mathrm{s}^{-1}$ in females compared to males in mature Fraser and Tompson River pink salmon (Williams and Brett 1987), by up to ~0.5 $\mathrm{BL}\cdot\mathrm{s}^{-1}$ in mature migrating adult Atlantic salmon (Booth 1998), and by ~0.2 $\mathrm{m}\cdot\mathrm{s}^{-1}$ in mature Schibetsu River pink salmon (Makiguchi et al. 2017). However, $U_{\max}$ was higher by an average of 5% in female Harrison River pink salmon (Clark et al. 2011), and U_{crit} was similar in male and Fraser River female sockeye (Farrell et al. 2003; Steinhausen et al. 2008; Wilson et al. 2013; Eliason et al. 2013*b*), Chilliwack lake coho salmon (Kraskura et al. 2021), and Shibetsu River chum salmon (Makiguchi et al. 2008). Here, we were unable to detect systematic differences in lab-reported swim performance between the sexes (Supplementary Fig. S4). Across all species, females' lab absolute swim speeds ranged between 37.00 and 237.60 $\mathrm{cm}\cdot\mathrm{s}^{-1}$, and males swam between 65.07 and 237.52 $\mathrm{cm}\cdot\mathrm{s}^{-1}$ ($N(\text{unspecified}) = 729$, $N(\text{females}) = 298$, $N(\text{males}) = 397$). Additionally, we found no correlation between gonad mass, or gonadosomatic index (GSI) and individual swim speed (Supplementary Fig. S5BC). The next step will be to specifically examine if sex-specific differences in adult salmon swimming are related to species, population-specific, or individual variation in maturity state (i.e., degree of sexual secondary characteristics, such as kype and dorsal hump, that can alter hydrodynamics).

In the field, there is evidence that female swimming capacity may be lower compared to males, which could further contribute to female-biased mortality rates (Bowerman et al. 2018; Hinch et al. 2021). However, we could not confirm any consistent trends from the field data (Supplementary Fig. S4). Across all species, female field swimming speeds ranged between 35.99 and 749.26 $\mathrm{cm}\cdot\mathrm{s}^{-1}$ ($N = 61$), and male field swimming speeds varied between 6.46 and 631.36 $\mathrm{cm}\cdot\mathrm{s}^{-1}$ ($N = 143$; Supplementary Fig. S4; deficient data at species or population levels). However, others have demonstrated sex-specific migration behaviours and capacities. Specifically, male Atlantic salmon in Sweden were more likely to choose optimal flows compared to females (53% females, 63% males; Lindberg et al. 2016), while female Gates Creek sockeye salmon were 9%–13% less likely to pass fishway compared to males (Roscoe et al. 2011; Burnett et al. 2014*b*, reviewed by Hinch et al. 2022). However, there is no clear evidence that bursting speeds in female adult salmon are lower than in males (e.g., Booth 1998; Hinch et al. 2002); Supplementary Fig. S4), though anaerobic recruitment and capacities may differ between sexes (Burnett et al. 2014*b*). Additionally, females appear to be more energy conservative compared to males traversing fast flows (e.g., Fraser River pink and sockeye salmon; Rand and Hinch 1998; Standen et al. 2002). Swim performance can diverge between male and female adult salmon as they mature *en route* to their spawning grounds. Specifically, in Exploits River, NL, Canada, Atlantic Salmon U_{crit} was lower by 0.5 ~ $\mathrm{BL}\cdot\mathrm{s}^{-1}$ in fully mature females compared to fully mature males, while burst and sustained swimming did not differ between sexes at any maturity state (Booth 1998). Alternatively, in Fraser River pink salmon, U_{crit} differed based on the fish's maturity state, but inconsistently across sexes (Williams and Brett 1987). Possibly, swim performance changes interactively with sex and maturity (Plaut 2002; Cooke 2004; Svendsen et al. 2009) or emerges only under multi-stressor conditions (reviewed by Hinch et al. 2022).

Various factors could drive lower swim performance in females compared to males. For example, migrating females and males undergo different morphological changes that alter their hydrodynamics (e.g., females change in circumference, males develop dorsal hump and kypes; Booth 1998; Conradsen and McGuigan 2015); females may have a lower aerobic metabolic scope (Clark et al. 2011) and divert more of their aerobic capacity towards gonad development and maintenance (Fenkes et al. 2016). Additionally, migrating females have elevated cortisol levels that can impair their recovery from strenuous swimming (Pagnotta et al. 1994; Hruska et al. 2010; Eliason et al. 2020; section *Recovery*). The extent to which female and male swimming performance differs and "why" are unresolved questions (e.g., Supplementary Figs. S4 and S5). However, they are crucial to predict population stability and dynamics of salmon species that have a once-in-a-lifetime chance to spawn (Hanson et al. 2008*b*).

Recovery

Fatigued and exhausted fish must recover following strenuous swimming (Kieffer 2000; Kieffer 2010; Holder et al. 2022; Birnie-Gauvin et al. 2023). During recovery, fish replenish their energy stores (oxygen, ATP, glycogen, and phosphocreatine), restore baseline metabolite levels (plasma and muscle lactate, plasma glucose) and other hormones to their baseline levels (cortisol), and reestablish ion, osmotic balance, and blood pH (clear CO_2, plasma K^+, Cl^-, and Na^+) (reviewed by Wood 1991; Milligan 1996; Kieffer 2000; Zhang et al. 2018;

Holder et al. 2022). The required investment in recovery (time and energy) depends on the magnitude of the swimming effort or exertion and duration of swimming (e.g., McDonald et al. 1998). It is unclear how much anaerobic swimming pushes individuals beyond the point of recovery, ultimately causing mortality (Black 1958; Wood et al. 1983; McLean et al. 2016; Hvas et al. 2021; Holder et al. 2022). Moreover, it is also unclear how much recovery is necessary for wild salmon to return to their normal activity, though several studies using U_{crit} tests have shown that adult salmon can repeat their swim performance after 45 min and without fully recovering to baseline levels (i.e., maximum metabolic rates only decreased to around ∼50%; Jain and Farrell 2003; Jain et al. 1998; Farrell 2008; Farrell et al. 1998; MacNutt et al. 2006; Wagner et al. 2006; Eliason et al. 2013*b*; Kraskura et al. 2021). Adults utilize several tactics (swimming and recovery behaviours) at the most challenging sections of migration. For example, salmon may use "accelerate-then-coast" or "burst-then-sustained speed" swimming patterns, swim slowly before the rapids, and minimize time during passage, while some (typically unsuccessful) salmon exhibit unsustainable anaerobic hyperactivity during passage (Hinch and Bratty 2000). Each of these swimming patterns define different swimming effort and recovery strategies. Possibly, there is a trade-off between repeat performance (rapid recovery) and the maximum bursting ability leading to different swimming and recovery patterns in the field.

Some insight about the required recovery time after various levels of swimming activity is gained from measuring blood and muscle tissue biochemistry, and observing behavioural recovery (Kieffer et al. 2011). Results from several studies on salmonids suggest that post-exercise plasma lactate levels that exceed 10 $\mathrm{mmol \cdot L^{-1}}$ may serve as an early warning sign for inability to recover and mortality (Farrell et al. 1998; Cooke et al. 2006, 2012; Eliason et al. 2022). Elevated temperature accelerates the accumulation of plasma lactate, thus exhaustive swimming under warming may be particularly alarming in the face of climate change (Kieffer et al. 1994; Gale et al. 2011). Additionally, successful migrating sockeye salmon had lower plasma glucose levels compared to unsuccessful fish (*en route* mortalities) (Cooke et al. 2006; Roscoe et al. 2011). Another early sign of exercise-related delayed mortality may be an individual's inability to recover their heart rates to their pre-exercise levels (Eliason et al. 2013*b*; Prystay et al. 2017; Bjarnason et al. 2019; Hvas et al. 2021; Doherty et al. 2022). These indicators, in addition to research activity to better understand recovery and post-exercise mortality in fish, will help us better understand how much anaerobic bursting leads to unrecoverable physiological disturbance that affects fish's behaviour.

Factors like larger body size, elevated temperature, and sex (especially females) could affect a fish's ability to recover. For example, larger salmonids had more disturbed osmo- and ion-balance than smaller fish (Ferguson et al. 1993; Clark et al. 2012; Kieffer 2000, but see: Oldham et al. 2019), and larger fish needed longer and more metabolically costly recovery after strenuous anaerobic exercise (McDonald et al. 1998; Clark et al. 2012). Post-exercise recovery can be drastically impaired under supra-optimal temperatures in adult salmonids. In elevated temperatures, salmon take longer to recover their aerobic metabolic capacity (Van Wert et al. 2023; Kraskura et al. 2021), heart rates (Prystay et al. 2017), and have impaired recovery of blood metabolites (e.g., cortisol: Gale et al. 2011; Raby et al. 2015; lactate: Gale et al. 2011; Kieffer et al. 1994; Van Wert et al. 2023; glucose: Gale et al. 2011). Further, female-biased mortality, particularly after exhaustive swimming, may be due to their inability to recover. Compared to males, female sockeye salmon took longer to recover elevated cardiac lactate levels post-exhaustion (Eliason et al. 2020), where one contributing factor could be lower cardiac lactate dehydrogenase activities in females than males (e.g., coho salmon: Little et al. 2020). Additionally, compared to males, females had higher plasma lactate levels at 0.5–1 h post-exhaustive exercise (sockeye and pink salmon: Donaldson et al. 2014; Eliason et al. 2020), higher plasma glucose levels (sockeye salmon: Gale et al. 2011; Donaldson et al. 2014), and plasma $\mathrm{K^{+}}$ levels for up to 4 h after exercise (Donaldson et al. 2014; Eliason et al. 2020). Higher lactate, glucose, and plasma potassium levels, as well as the total metabolic costs, all indicate either a higher anaerobic effort or impaired recovery processes. In fact, Burnett et al. (2014*b*) found that sockeye females used more anaerobic swimming than males passing high flows in the field. However, the direct links between these physiological indices, bursting activity (e.g., speed and frequency of burst), and their interactions with covariates like body size and sex remain to be established.

This review does not provide quantitative data on post-swim recovery performance. Instead, we qualitatively reviewed each included study to gauge the extent to which recovery was considered (Supplementary Table S3). Of 103 studies, 34 studies discussed but did not experimentally evaluate recovery in the context of fish's swim performance. Twenty-eight studies measured one or more recovery performances in adult salmon, between which blood biochemistry was the most common approach (19/23 studies). Specifically, recovery performance was measured by testing plasma ion and metabolite levels (plasma $\mathrm{Cl^{-}}$, $\mathrm{K^{+}}$, $\mathrm{Na^{+}}$, osmolality, glucose, lactate, cortisol, sex hormones [estradiol and testosterone]), blood oxygen levels (e.g., arterial and venous blood oxygen levels), and hematocrit and hemoglobin levels. Four out of 28 studies measured post-exercise excess oxygen consumption rates (total metabolic costs of recovery), and 17/23 studies did repeat swim performance tests with a minimal recovery time (∼1 h). Paulik and DeLacy (1957*a*) did time to fatigue repeat swim tests with 6 h recovery in between the tests demonstrating that adult pacific salmon can repeat their fatigue swim performance. Lastly, cardiovascular physiology during recovery was examined in 11 studies. Some studies adopted multiple approaches to explore recovery performance in fish (e.g., Farrell et al. 1998; Wagner et al. 2005; Eliason et al. 2013*b*). For example, a better understanding of optimal recovery conditions for adult salmon and other species could be described by studying behavioural recovery (e.g., better recovery when fish were swimming under low flow; Kieffer et al. 2011). More holistic knowledge of maximum swimming performance in migrating species will require studies that couple measurements of anaerobic swimming capacity, including speeds, repeatability, and recovery performance.

What are the next steps?

As the field of fish swimming continues to grow, we identified a central need to better understand maximum anaerobic swimming performance and the contingent trade-offs, like physiological recovery, in adult salmon. Swimming is a multifaceted performance and therefore we recommend performing multi-metric assessments of fish swimming where the set of metrics that comprise swimming performance are clearly defined (e.g., duration of swimming, speed, acceleration, ground speed, speed through the water, cost of transport, and in the context of exogenous and endogenous factors, behaviour and morphology) (see Table 1 in Castro-Santos et al. 2022 for metrics in fish locomotion). This approach could prove particularly valuable in systems where fish swimming or migration responses differ because operating trade-offs result in lower performance in one trait (e.g., maximum swimming speed) but higher performance in others (e.g., higher recovery rate and repeat swimming) with net equal fitness among individuals displaying different tactics. Therefore, different aspects of swimming performance, including maximum swimming speeds, can directly link to individual fitness, population growth rates, and sustainability.

Lab studies on swim performance under a controlled setting have solidified that swimming varies across salmon species (Lee et al. 2003*b*, 2003*a*), populations (Eliason et al. 2011), and individuals (Clark et al. 2011), depending on various intrinsic factors (exposure to environmental toxicants, infections rates, maturity states, aerobic state; Supplementary Table S1 and Fig. S6) and extrinsic factors (migration duration, difficulty, discharge, and predation, Fig. 4A) (Fig. 1). Field studies provide invaluable information about adult salmon's maximum swimming capacity and their swimming behaviour in the wild (Cooke et al. 2013; Brownscombe et al. 2018; Matley et al. 2022). However, future lab and field studies are required to fill in the currently fragmented knowledge base of maximum swim capacity in adult salmon. Below we outline a few emerging research questions identified from this review:

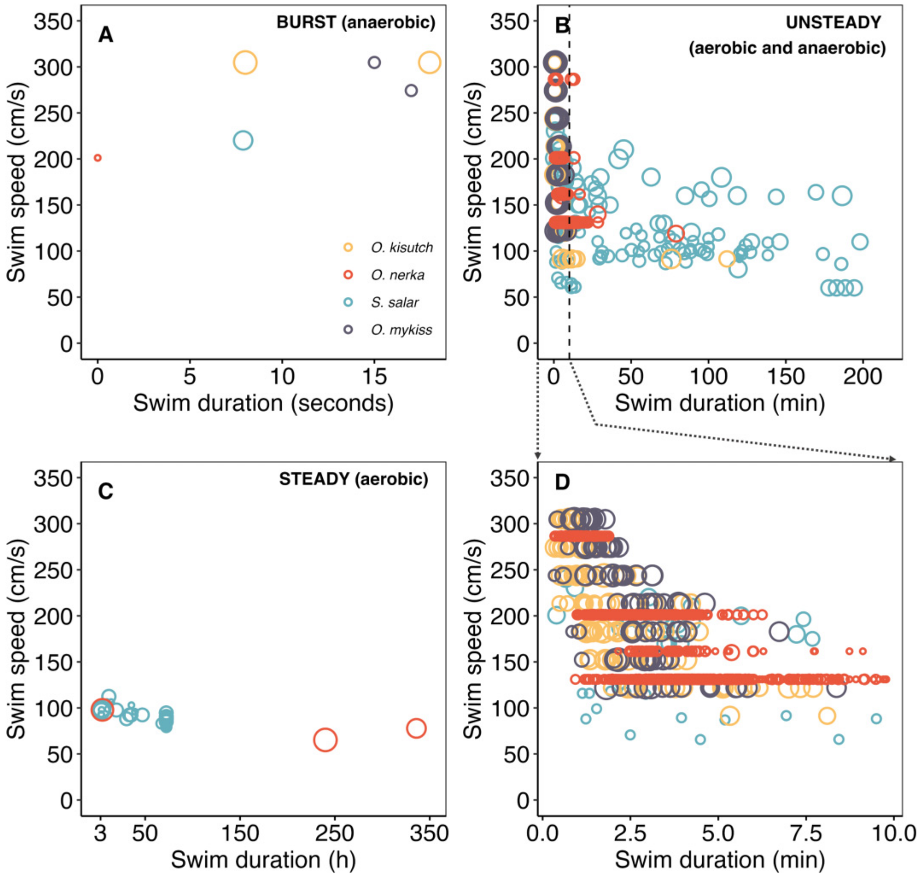
1. What is the bursting capacity and behaviour in adult salmon, across and within species?
   a. What is the maximum anaerobic swimming speed ($cm{\cdot}s^{-1}$, $cm{\cdot}s^{-2}$)?
   b. How long (duration) can a fish sustain its maximum swim speeds (seconds) (expand data set in Fig. 9)?
   c. How frequently can adult salmon burst under high flow conditions in the wild (e.g., bursts/min)
   d. How much can bursting, or maximum anaerobic activity, be sustained and not lead to post-exercise or premature mortality (duration and frequency)?
2. What is the recovery capacity of adult salmon, across and within species?
   a. How much recovery is necessary to repeat burst swim performance?
   b. What physiological metrics indicate a sufficient recovery from exhaustive anaerobic swimming? (e.g., recovery of blood pH, lactate, glucose, cortisol, and potassium levels to a certain level of pre-exercise baseline; recovery of fish's maximum metabolic rates or aerobic scopes, heart rate, HSP expression levels, and transcriptomics profiles)
   c. What physiological metrics flag post-exercise mortality?
   d. What are optimal recovery conditions (e.g., water velocities, temperature, and duration)
3. What biological (intrinsic) and environmental (extrinsic) factors determine bursting capacity, behaviour, and recovery in wild adult salmon? (e.g., temperature, sex, size, turbulence/flow, hypoxia, group or individual swimming, maturity state, injury or infection, and multi-stressor scenarios) (Fig. 1) (expand dataset in Supplementary Fig. S6)

Testing burst swimming in the laboratory and field

Fish swim performance can be measured using various tests, but few are designed to measure anaerobic swimming, especially for large fish like adult salmon. A few valuable but rather uncommon approaches that have been used across fish species include: (i) gait-transition tests in large raceways (Paulik and DeLacy 1958; Peake 2008; Marras et al. 2010), (ii) swim performance tests in custom-designed raceway systems with controllable turbulent conditions resembling natural structures (Nikora et al. 2003; Hockley et al. 2014; Li et al. 2022), (iii) sprint swimming tests on a drag strip (Reidy et al. 2000; Nelson et al. 2002; Haro et al. 2004; Starrs et al. 2011; Castro-Santos et al. 2012, Martínez et al. 2002, also see flume design in Paulik and DeLacy 1958), and (iv) jump and leap performance tests in tunnel-type adjustable waterfalls (Kondratieff and Myrick 2006; Lauritzen et al. 2010). Currently, U_{crit} and U_{max} remain the dominant swimming tests, but as the database of maximum swimming speeds (speed through the water, $cm{\cdot}s^{-1}$) measured using other approaches grow, it could prove valuable to develop "correction" or "conversion" factors that predict the maximum burst speeds from commonly reported U_{crit} speeds. Additionally, studies on juvenile fish can inspire future multi-metric studies on maximum swimming capacity in adult salmon (Kieffer et al. 2011; McDonald et al. 1998). For example, McDonald et al. 1998 used three approaches with different swimming time and intensity domains (manual chase, TTF, U_{max}) to specifically examine anaerobic capacity and recovery in fish across sizes. Notably, different swim tests have different limitations including their scaling with body size, levels of anaerobic expenditure, and behaviour of fish during swimming and recovery (McDonald et al. 1998; Kieffer et al. 2011). Nevertheless, incorporating these approaches in future adult salmon studies will help elucidate some of the unresolved questions described above.

Accurately measuring fish swimming speeds in the field and under high water velocities is difficult. Even still, most reported burst speeds come from field studies, particularly those that used EMG tags. However, the technology to track fish speeds and acceleration in the wild is growing rapidly (Matley et al. 2022; Wilson et al. 2022; Warren-Myers et al. 2023). Accelerometry can be particularly useful for measuring fine-scale anaerobic swim speeds (e.g., $> 300\ cm{\cdot}s^{-1}$;

Fig. 9. Time-to-fatigue relationships across species. Different panels show how time to fatigue varies across species (colours) depending on if the fish are using (A) anaerobic burst swimming (<20 s) (B) unsteady swimming modes, capturing a combination of aerobic and anaerobic swim speeds (panel (D) is a "zoomed"-in section of panel (A)). (C) aerobically swimming (lasts hours to days). The size of each symbol represents the size of the fish (length); larger symbols belong to larger fish (size range: 37.47–81.92, mean = 45.08 cm length).



Fuchs and Caudill 2019) in the field across greater velocity ranges (Wilson et al. 2022). Recent developments have shown that fish swimming speeds and energetics (e.g., metabolic rates and heart rates) may be estimated using tail beat frequencies and tail beat amplitude (thurst), which could be observed using non-invasive methods like video analysis (Warren-Myers et al. 2023). Though, these methods must be refined by including burst speeds, scaling coefficients with body size, and swimming in different ecological settings (Warren-Myers et al. 2023). Additionally, a recent review by Bett et al. (2022) demonstrates how measuring swim performance in regulated natural experimental systems like Seton Dam within the Fraser Watershed can provide key information for management and conservation of salmon (Bett et al. 2022 and references within).

Management and conservation

The main impetus for this review was a response to a natural disaster (the Big Bar Landslide which occurred in British Columbia, Canada in 2018), and the requirement of fisheries biologists to provide the latest information on the maximum swimming capacity of adult salmon to managers, to determine the best mitigation measures to maximize survival past the landslide for numerous imperiled salmon populations (Big Bar landslide response, Government of Canada 2019). Almost immediately, the landslide created a short, steep hydraulic drop that culminated in an overfall of up to 7 m in height, spanning across the entire river. Rock manipulation and high natural high flows reduced the overfall height but caused the length of the migration barrier to extend to over 100 m along one bank that was potentially passable to salmon. Moreover, this created a series of fast-flowing microhydraulic features with variable encounter velocities that changed with river stage height. Whether salmon could successfully overcome these series of barriers at a given stage height was unknown at the time, given a lack of knowledge on the maximum swimming abilities of adult salmon, especially in regard to maximum absolute speeds and maximum duration for a given swim speed (Fig. 9). Given the acute nature of this event and immediate conservation concerns, it was impractical to build 3-D hydraulic river models (Goodwin et al. 2014) and to carry out long-term experiments to determine maximum swimming capacity in different species of salmon. Within this context, the information generated in this review can help direct future research in this field, as well as provide a summary of the current state of knowledge for future events.

Mitigation of natural landslides is an important application of this work, but a more ubiquitous application of this information would be in the building of effective fish passage structures with consideration of different species, body sizes, sex, maturity states (and life stages), temperatures, and other ecologically relevant contexts (e.g., Haro et al. 2004; Castro-Santos 2006; Newbold et al. 2016; Dockery et al. 2017*a*; Silva et al. 2018; Katopodis et al. 2019; Matica 2020). Although much work has been devoted to this area of applied research, structured fishway development approaches that explicitly and systematically incorporate maximum swim performance of fishes are rare (Castro-Santos 2006; Turek et al. 2016; Birnie-Gauvin et al. 2019). Some approaches have been experiential (Birnie-Gauvin et al. 2017), many repeat structures or designs that have previously worked (Hatry et al. 2013; Hershey 2021) despite being designed for species with different maximum swimming capacity (Birnie-Gauvin et al. 2019), and fewer focus on gaining a deeper understanding of the contexts that make fish passage successful or not, including maximum swim performance as well as recovery capacity (Castro-Santos 2006 variable speeds; Reiser et al. 2011; Birnie-Gauvin et al. 2023). A shortcoming to numerous existing fishways is their focused design that suits economically favourable species like salmonids—which are comparatively strong swimmers (Eliason and Farrell 2016)—thus neglecting interspecific variation in swimming performance, specifically disfavouring weaker swimming species that also suffer from habitat fragmentation (Birnie-Gauvin et al. 2019; Jones et al. 2020; Dolson et al. 2023). Even when designed for salmon, the current approach lacks the practical acknowledgment of interspecific and intraspecific variation in swimming performance, which can vary by sex, size, temperature, and endogenous energy reserves (Booth et al. 1997*a*; MacNutt et al. 2006; Clark et al. 2012; Makiguchi et al. 2017; Lennox et al. 2018*b*; Van Wert et al. 2023). Therefore, the interindividual variation in swimming across and within species warrants more study as it could be particularly important for maintaining stable populations. A re-evaluation of current fish passage literature using the information gathered in this review could prove valuable for advancing our understanding of the links between maximum swimming capacity and fish passage success, and the factors that may influence these links.

Another intriguing application of this work is for conservation hatcheries that have emerged in response to acute mortality events, such as those caused by landslides, for reintroductions into blocked upper watersheds, or to reverse current population declines (Flagg and Nash 1999; Brown and Day 2002). There is very little known about the links between genetics and migration ability, and whether breeding programs could have negative (or positive) impacts on swimming capacity (e.g., Chittenden et al. 2010). We are learning more about the transcriptomic responses to adverse environmental conditions, such as temperature, that can influence swim performance (e.g., Jeffries et al. 2012, 2014; Robinson et al. 2017; Bowen et al. 2020). However, we do not yet know whether genomic responses are preserved along the migration route (as fish mature and become progressively more energy-depleted), nor do we know the genetic basis for these transcriptional changes. Currently, the strongest known genetic signature in relation to migration are genes associated with migration timing (e.g., Prince et al. 2017), which determine the time when fish arrive to dams, fishways, or other challenging structures (Willis et al. 2021). Breeding programs that do not consider differences in the genetic basis for traits related to maximum swim performance of salmonids across different life stages, including adult migrants, run the risk of not achieving their conservation goals.

Other conservation applications of this work are related to predicting migration ability in association with changes in habitat conditions stemming from human intervention and climate change processes. An example of the former is the current momentum to remove dams in rivers systems, such as the Elwha River (Washington State, US; Liermann et al. 2017; NOAA Fisheries 2021), Klamath River (Oregon, Northern California, US; Klamath River Renewal Corporation 2020), and Snake River dams (Pacific Northwest, US; Storch et al. 2022), to restore connectivity and re-establish self-sustaining salmon populations (Liermann et al. 2017; Duda et al. 2021). If we predict what the river geomorphology and hydrology will be like post-removal, then we can make predictions about the ability of salmon to migrate upstream, as well as their distribution limits based on maximum swimming ability data, adjusted for size, sex, species, and temperature. Climate change is changing the hydraulic and thermal conditions of river systems across systems (e.g., Fenkes et al. 2016; Islam et al. 2019; Howard and von Biela 2023), with consequences on the migration ability of fishes, including salmon (Hague et al. 2011; Reed et al. 2011). As climate change-related events increase in frequency and severity, the glacial retreat may provide a potential for range expansion in salmon (Pitman et al. 2021). Researchers have identified new riverscapes for potential exploitation by salmon, but whether salmon exploit these new habitats or not will partially depend on whether their maximum swim performance and consequential recovery needs are suited to these systems. These are few examples of how and why a better understanding of maximum swim performance is key for predicting success, determining adequate mitigation measures, and meeting overall conservation goals.

Conclusion

Adult salmonids are exceptional swimmers that can achieve anaerobically fueled burst speeds up to 800 $\text{cm}\cdot\text{s}^{-1}$ and 13 $\text{BL}\cdot\text{s}^{-1}$ during their migration (Fig. 4, Fig. 5, and Table 1). However, each burst may only last a few seconds and can only be repeated a limited number of times before fish must recover. Although migrating adult salmon routinely swim at much lower aerobic swim speeds, <200–250 $\text{cm}\cdot\text{s}^{-1}$ (<2 $\text{BL}\cdot\text{s}^{-1}$), it is critical to understand their anaerobic swim capacity to develop effective management, conservation, and mitigation efforts that support the success of iconic salmon. Future studies that measure swim performance in salmon may bring us closer to the currently unresolved question: *how fast and for how long can salmon swim?*

The results of this review show that most measured swim speeds in adult salmon were within aerobic speeds or at borderline aerobic and anaerobic (burst and coast) speeds. Specifically, most reported speeds are from critical swim speeds (U_{crit}) or field-recorded speeds, which vary remarkably between species. Although swim performance in adult salmon is known to vary at the population level, systematic differences were not detectable due to data deficiency, interindividual variation, and possibly study biases. Sockeye salmon was the most-studied species, while the least studied were larger body chum salmon and Chinook salmon. Further, swim performance was clearly sensitive to temperature, and these differences were species-specific. It must be stressed that the thermal physiology underscoring swimming ability is population-specific; thus, the reported optimal temperature for swimming should be interpreted with caution. Reliable estimates of maximum swim performance ($\mathrm{cm \cdot s^{-1}}$) at inter-and intraspecific levels cannot be provided without additional sex-specific data that particularly covers large-size species, broader temperature ranges, and the maturity of fish.

Glossary

Aerobic metabolism	A cellular process that produces energy (ATP) from glucose, fatty acids, and amino acids in the presence of oxygen.
Anaerobic metabolism	A cellular process that produces energy (ATP) using glucose and glycogen without oxygen.
Burst (sprint) swimming	Swimming at high tailbeat frequency and amplitude, which generates highest thrust and velocity, quickly results in anaerobic muscle respiration, and is associated with predator avoidance, jumping, and mating and spawning activities. Bursting is an unsustainable, physiologically exhausting swimming mode that quickly leads to fatigue.
Burst and coast (burst and glide)	A transitional swimming mode that consists of alternating periods of accelerations (burst) and unpowered, passive gliding (coast or glide).
Exhaustion	A physiological state when an individual's energy reserves are depleted and an individual is unresponsive to stimuli motivating swim activity. An exhausted fish cannot immediately continue swimming, but may be able to right itself and display slow swimming after short recovery (minutes).
Fatigue	A physiological state and behavioural response at which an individual's ability to maximally swim (burst) is severely reduced. Fatigued fish have lost motivation to swim but may continue to swim at low speeds with limited ability to respond to stimuli.
Prolonged (unsteady) swimming	A combination of aerobic and anaerobic swimming. During this unsteady swimming mode, continuous (aerobic) swimming is intersected with rapid bursts, turns, and consecutive burst-and-coast episodes (anaerobic). It will eventually lead to fatigue.
Sustained (steady) swimming	Aerobic swimming that can be maintained for weeks to months. This swimming activity is used for daily behaviours, foraging, exploring new environments, hovering, and steady swimming against low flows. It does not lead to fatigue.
Time to fatigue swimming	Swimming test or approach, where fish swims at a constant (pre-determined) velocity until it reaches fatigue.
$\boldsymbol{U_{\mathrm{crit}}}$	(Test) is an aerobic and anaerobic swim performance test where water velocity is incrementally increased in a stepwise manner and held at that speed for a pre-determined time (often 20 min). The U_{crit} test is performed in a swim flume, and the protocol is most commonly used to examine swimming energetics (oxygen consumption rates, a

	proxy for metabolic rate). The U_{crit} test estimates the critical swim speed (cm·s^{-1}, U_{crit} swim performance metric) which is calculated using the top swim velocity at which fish reached fatigue, the duration the fish swum at the top speed, the velocity difference between stepwise increments, and the time difference between stepwise velocity increments.
U_{max}	(Test) is an aerobic and anaerobic swim performance test similar to U_{crit}, but the water velocity is continuously increased throughout the test (often between 1 and 10 cm·s^{-1}·min^{-1}) and metabolism is typically not measured during the swim trial. The maximum swim speed (cm·s^{-1}, U_{max} swim performance metric) is the highest swimming speed that the fish can achieve.

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Data availability

All data and code used to synthesize the data are available on GitHub repository: https://github.com/kraskura/KK_et_al_salmon-swim-BigBar. Available are (i) the main dataset that was used to produce all figures and generate tables (ii) data and statistical analysis R code, (iii) annotated figures from original publications that were used for data extraction, (iv) the .csv files with the corresponding coordinate data (x, y cord., px), and (v) an excel sheet with calculations to obtain swim speed data (cm·s^{-1} or BL·s^{-1}) from tracked coordinates.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2023-0246.

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APPENDIX A

Meta-analysis methods

Swim speed can be described using two units, the absolute swim speed units (cm·s^{-1}, m·s^{-1}) and relative swim speed units using body length of the fish (BL·s^{-1}). The absolute swim speed is directly comparable across observations and is a more relevant metric in context of natural conditions (e.g., river flows). On the other hand, relative swim speed has merits when considering the swimming physiology and transition states from aerobic to anaerobic swimming. Where possible, both absolute and relative swim speeds were compiled for our analysis alongside with body length of the fish (cm). To obtain the most comprehensive outlook of swimming capacity of salmon applicable to ecologically applied settings, we estimated absolute swim speeds where possible, but it must be noted that these estimates contain error. The directly reported and estimated absolute swim speeds are visually discrete in our data presentation.

Data search and selection

Systematic and comprehensive review was performed using Web of Science and Google Scholar (https://scholar.google.com/). To complete a systematic review, we used Web of Science with access through University of California, Santa Barbara in 2020 April, and in January 2022. We queried articles published between 1950 and 2022 using five specific searches using keywords *"speed," "salmon," "swim," "burst," "jump," "leap," "sprint," Ucrit, Umax, Ucat, critical swim, maximum swim, adult*" appear in all fields (keywords appear anywhere in the full record), and where keywords "*juvenile*" do not appear in topic fields (abstract, title, and author keywords). Search details and number of returns are summarized in Table A1. The comprehensive and cross-reference review through Google Scholar was performed between December 2019 and April 2020 using keywords in various combinations (examples: *"Pacific salmon swim", "Salmon sprint", "Salmon jump", "Salmon anaerobic swim", "Salmon Ucrit", "Salmon burst swim", "Columbia River salmon swim",* and *"Adult salmon swim"*). Each of different search phrases were used to query literature published between 1950 and 2020. The number of returned reports or literature ranged anywhere from 3 (e.g., "salmon Ucrit" in 1961–1970) up to a several thousand ("Pacific salmon swim" in 2001–2010 resulted in $\sim$ 10 700 returns); results were assessed until at least 30 consecutive results (three pages) became irrelevant for the goal of this study (most cases $>$ 100 results were assessed; details on this search including keywords, time ranges, date of the search, and notes on number of returns are summarized in Table A2).

The retained articles from systemic and comprehensive search were individually assessed against our criteria for inclusion or exclusion in our database; the criteria were: (i) quantitative swimming speed of fish (groups or individuals) must be reported either in text, table, or be plotted, (ii) swim speed must belong to Pacific salmon (*Oncorhynchus spp:* sockeye salmon (*O. nerka*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), chinook salmon (*O. tshawytscha*), rainbow or steelhead trout *(Oncorhynchus mykiss*), and Atlantic salmon, (*Salmo salar*), (iii) exclude migration speeds reported on km/d or similarly coarse scales, (iv) fish must have reached an adult life stage (Pacific salmon *Oncorhynchus* spp. $>$ 800 g; *O. mykiss* $>$ 500 g; Atlantic salmon *S. salar* $>$ 500 g; or fish $>$ 30 cm when mass was not reported). Selected studies were individually reviewed to extract targeted information to build the database. Data only presented through figures were digitized using ImageJ v 1.52 (Schneider et al. 2012), to extract reference values on *x*- and/or *y*-axis, and swim data points (all in px). All tracks were saved and used to calculate swim speed (in some cases also, temperature, swimming speeds, and body size of the fish were obtained from original author published figures).

Database variables

A goal of this review was to link swimming capacity with environmental conditions and condition of the fish. We compiled different types of entries to ensure all-encompassing database of salmon swimming capacity. An entry of swim speed can represent a mean swim performance value of a group of individuals ($n > 1$ salmon, commonly reported), or a swim speed measured in an individual fish ($n = 1$);

Table A1. Summary details of systematic review using Web of Sciences.

SEARCH ID1:	
(ALL=(speed* AND salmon* AND (burst* OR jump* OR leap* OR sprint*) NOT TS = juvenile) AND LANGUAGE: (English)	
Returns (*N* studies) and year or the search	55 (April 2020) 64 (January 2022)
Included (*N* studies)	8 (no additions in 2022)
SEARCH ID2:	
(ALL=(speed* AND salmon* AND swim* AND (Ucrit OR Umax OR Ucat) NOT TS = juvenile) AND LANGUAGE: (English)	
Returns (*N* studies) and year or the search	16 (April 2020) 18 (January 2022)
Included (*N* studies)	4 (3 added in April 2020, 1 added 2022)
SEARCH ID3:	
(ALL=(speed* AND salmon* AND swim* AND (critical swim OR maxim* swim) NOT TS = juvenile) AND LANGUAGE: (English)	
Returns (*N* studies) and year or the search	252 (April 2020) 265 (January 2022)
Included (*N* studies)	30 (28 added in April 2020, 2 added in 2022)
SEARCH ID4:	
(ALL=(speed* AND salmon* AND swim* AND adult AND (critical swim OR maximum swim) NOT TS = juvenile) AND LANGUAGE: (English)	
Returns (*N* studies) and year or the search	46 (April 2020) 45 (January 2022)
Included (*N* studies)	19 (all additions from 2020 search)
SEARCH ID5 *(only 2022)*:	
(ALL=(adult AND salmon* AND (swim fatigue OR time to fatigue OR endurance swim))	
Returns (*N* studies) and year or the search	25 (January 2022) **This search was performed to specifically query studies measuring time to fatigue performance in salmon.*
Included (*N* studies)	0

to specify the type of entry, we created a descriptive variable “group” or “individual”. For some studies, there were more than a single datapoint reported for one individual or a group of salmon (for example, repeat swim speed tests, or one individual migrating through different sections of the river). The non-independence and weight of the data (sample size, $n = 1$ or $n > 1$) are considered in primary analyses and inference.

Following our aim to investigate intra-specific variation in swim performance of salmon, we reported the origin of the fish. This was categorized at two levels, (i) specific origin of fish (e.g., stock or population, specific collection site, a specific hatchery or farm, or a study site), (ii) a coarse scale classification of origin [“collection” (all entries with noted collection site as best estimate of their origin), “farm,” “hatchery,” “stock” (population), “study” (location of the study, not a reliable metric of fish origin)].

We reported methods used to obtain swim speeds of salmon (swim performance test methods) and the mean temperature during these swim tests. Swim performance tests were defined following an established terminology in fish swimming literature. Swim tests performed under controlled, predominantly, laboratory setting include, “U_{crit}”—critical swim speed test, “U_{max}”—maximum (constant acceleration) swim speed test, and “TTF”—time to fatigue tests or endurance swim tests. We used a category “Field” to describe swim performance measured in migrating fish, and category “Jump” to describe velocity of jumping fish. We compiled swim performance measured using non-traditional methods in a category “Swim” includes. The compiled swim test categories are detailed in Table A3. Test temperature represents the reported water temperature in the swim tunnels, flumes, tanks, or the mean reported river water temperature from the field tracking studies. Caution may be used when drawing any strong conclusions on temperature effects of swim performance, because the mean temperatures are often not directly representing what fish may have experienced, especially in the field studies.

A selection of additional variables that are known to influence fish swimming performance and that we included in the database when available include: *intrinsic fish condition, extrinsic fish condition, sex, salinity, surgery and instrumentation, quantitative measures of maturity, water flow velocity and/or discharge, mortality, and tracking versus laboratory study.* None of the latter outlined variables were included in the primary analyses due to their low sample sizes per category, but they are discussed in this review.

When possible, we extracted intrinsic fish condition, a variable specifying intrinsic state of the fish. It was used to group fish with similar physiological conditions in common

Table A2. Summary details of comprehensive review using Google Scholar.

Search terms	Date search was performed	Publication years (range)	Notes on reviews and returns
Pacific salmon swim	26 December 2019	1950–1960	Returned literature became irrelevant to our topic (other species than salmon, no swimming) starting at pages 10–13; search stopped.
Salmon burst			Unsuccessful search, literature not about fish. search stopped passed pages 3–4.
Salmon sprint			Unsuccessful search. Mostly irrelevant literature, search stopped passed page 1.
Burst swim adult trout	18 March 2020		About 761 results (0.08 s) (18 March 2020)
Salmon swim	26 December 2019	1961–1970	About 1130 results (0.04 s). No more relevant studies passed page 14, search stopped.
Salmon burst			About 805 results (0.13 s), by returned page 4; most of the relevant publications were already included in the dataset; others were irrelevant.
Burst swim			Unsuccessful search, returns are not about fish.
Salmon Ucrit			Three results (0.06 s), of which two were *Brett* papers, and one publication that cites and discusses the search term "in text."
Salmon swim Columbia river, USA	15 January 2020		About 720 results (0.05 s). Reviewed.
Salmon Ucrit	27 December 2019	1971–1980	Three results (0.04 sec), of which two were Webb papers, and one publication on sturgeon.
Salmon burst			About 1480 results (0.08 s). Starting at pages 5 and 6, all returns were on different fish species, or returned publications focused on irrelevant performances, e.g., behavioural studies only
Pacific salmon burst			About 1050 results (0.07 s). Mainly studies about Oregon coho salmon and trout, and tracking studies. Starting at page 9 mostly, studies were mostly about early stage salmonids, particularly trout (yearlings, fry), hatchery fish and development, and aquaculture.
Pacific salmon swim			About 1120 results (0.20 s); after page 15, returned literature was irrelevant.
Salmon swim Columbia river, USA			About 1450 results (0.10 s); after page 9, returned literature was irrelevant.
Pacific salmon Ucrit		1981–1990	12 results (0.11 s)
Salmon burst			About 3310 results (0.08 s)—Most studies were on Atlantic salmon. After page 8, no more relevant papers.
salmon jump			Starting page 12, no more—relevant studies regarding our goal; returned mostly studied on early life stage fish (especially, Atlantic salmon), and studies on other performances than swimming.
Salmon swim Columbia River			About 2200 results (0.13 s): reviewed 10 pages, returned already included studies; search stopped—no new literature added to our database.
Pacific Salmon Ucrit	28 December 2019	1991–2000	About 73 results (0.08 s). All studies reviewed. **This was the most successful and relevant search**
Salmon burst swim			About 3210 results (0.10 s); Starting at page 10—no more relevant papers.
Pacific salmon swim			About 4100 results (0.10 s); Starting at page 10—no more relevant papers, and studies on adult salmon.
Pacific salmon anaerobic swim			About 538 results (0.04 s); Starting at page 5—papers were still about swimming but on other fish species, not Pacific salmon.
salmon swim Columbia River			Starting at page 10, most studies were on smolts and juveniles.
Salmon Ucrit	30 December 2019	2001–2010	About 349 results (0.06 s); starting at age 6, search returns started to deviate from Pacific salmon studies, page 7 no more relevant papers.
Salmon anaerobic swim			About 4240 results (0.09 s); starting at page 9 no more relevant papers.
Pacific salmon swim			About 10 700 results (0.12 s)
Pacific salmon burst swim			About 4350 results (0.10 s); starting at page 6, no more relevant returns.
salmon swim Columbia River	19 March 2020		About 11 900 results (0.11 s); starting at page 12, literature mostly l on juvenile fish and other species.
Adult trout swimming	19 March 2020		About 15 400 results (0.14 s); Pages 13–17 returned no more studies on adult fish; stop search after page 18.
Adult Atlantic salmon swim	21 March 2020		About 14 500 results (0.12 s)

Table A2. (*concluded*).

Search terms	Date search was performed	Publication years (range)	Notes on reviews and returns
Pacific salmon burst swim	31 December, 21 March	2011–2020	About 5800 results (0.08 s); Pages 7 and 8 no more relevant studies, mostly other species. The search returned a lot of offspring burst swim capacity studies examining maternal effects on performance.
Salmon Ucrit			About 536 results (0.08 s); lots of repeated returns (from previous searches) and studies on Atlantic salmon
Pacific salmon anaerobic swim			About 2300 results (0.08 s); reviewed until Page 13, no more relevant studies, or studies that already were included.
Pacific salmon max swim speed			Unsuccessful.
Adult trout swimming	21 March 2020		About 17 100 results (0.08 s)
Adult Atlantic salmon swim			About 16 900 results (0.10 s)
Salmon swim Columbia River			About 13 800 results (0.09 s); reviewed 18 pages.
Columbia river salmon swim	14 January 2020	Not specified	About 28 700 results (0.28 s)
Burst swim adult trout	19 March 2020		About 61 500 results (0.07 s)
Swimming masu salmon	21 March 2020	Not specified	About 2600 results (0.09 s); Went through 5 pages, no relevant studies found (except one that was already reported: Miyoshi et al. 2014)

***Additional cross reference search was performed in January 2023, with particular focus on technical reports.*

Table A3. Summary of species-specific sample sizes and corresponding reference IDs.

	All entries in dataset		Entries: absolute swim speed (cm·s^{-1})		Entries: relative swim speed (BL·s^{-1})		Entries with both, relative and absolute swim speed	
Species	*N (n)*	*Ref. ID*	*N (n)*	*Ref.ID*	*N (n)*	*Ref.ID*	*N (n)*	*Ref.ID*
O. gorbuscha	**8 (216)**	**6, 9, 13, 20, 21, 24, 43, 88**	4 (58)	9, 13, 20, 43	7 (211)	6, 9, 13, 21, 24, 43, 88	3 (52)	9, 13, 43
O. keta	**7 (52)**	**39, 41, 42, 44, 88, 204, 214**	4 (14)	39, 41, 204, 214	5 (57)	39, 41, 42, 44, 88	2 (2)	39, 41
O. kisutch	**14 (409)**	**10, 13, 18, 17, 28, 45, 50, 54, 89, 12, 53, 213, 214, 216**	11 (364)	10, 13, 18, 17, 50, 54, 89, 53, 213, 214, 216	7 (148)	10, 13, 18, 28, 45, 89, 12	4 (103)	10, 13, 18, 89
O. masou	**1 (5)**	**44**			2 (23)	63, 44		
O. mykiss	**21 (318)**	**65, 68, 69, 72, 73, 74, 75, 76, 77, 80, 87, 90, 92, 94, 95, 205, 206, 53, 212, 215, 54**	12 (193)	65, 68, 69, 73, 76, 87, 95, 205, 53, 212, 215, 54	13 (134)	68, 72, 74, 75, 77, 80, 90, 92, 94, 95, 205, 206, 212	4 (9)	68, 95, 205, 212
O. nerka	**32 (1971)**	**1, 2, 3, 5, 19, 7, 8, 9, 13, 14, 15, 16, 20, 21, 22, 23, 29, 30, 31, 38, 47, 50, 54, 40, 58, 79, 12, 213, 11, 217, 27, [25, 26, 48]**	21 (1781)	1, 2, 3, 5, 7, 9, 13, 20, 29, 30, 31, 38, 50, 54, 40, 58, 79, 213, 217, 27, [25, 26, 48]	21 (499)	1, 3, 5, 19, 7, 8, 9, 13, 14, 15, 16, 21, 22, 23, 47, 46, 79, 12, 11, 27, [25, 26, 48]	9 (300)	1, 3, 5, 7, 9, 13, 79, 27, [25, 26, 48]
O. tshawytscha	**6 (83)**	**4, 36, 35, 37, 33, 53**	5 (81)	36, 35, 37, 33, 53	2 (9)	4, 35	1 (7)	35
S. salar	**25 (418)**	**55, 56, 57, 60, 62, 70, 71, 78, 81, 82, 83, 84, 85, 86, 61, 91, 93, 96, 100, 102, 104, 105, 201, 202, 203**	16 (233)	56, 57, 60, 62, 70, 78, 81, 83, 84, 85, 86, 61, 102, 105, 202, 203	16 (296)	55, 56, 71, 78, 81, 82, 84, 91, 93, 96, 100, 102, 104, 105, 201, 203	5 (111)	56, 78, 81, 84, 203

Notes: Provided are summaries for absolute and relative swim speeds (BL·s^{-1} and cm·s^{-1}, and studies that report both BL·s^{-1} and cm·s^{-1}). Ref. ID, Reference ID number, the matched references list is provided in Appendix B. *N*, number of studies; *n*, number of entries in database.

Table A4. The summary of swim tests defined in the data.

Condition	Subcategory of the condition	*N* (*n*)	Ref. ID	Description
Field	Field	15 (350)	5, 20, 21, 29, 30, 31, 36, 35, 39, 41, 47, 50, 63, 87, 88	Swim speeds reported during migration in the field.
Fishway	Fishway	9 (114)	8, 22, 23, 38, 44, 46, 56, 53, 214	Swim speeds reported of fish passing established fishways.
Jump	Jump	2 (9)	40, 58	Jump velocity of fish; this includes horizontal, vertical, total, and take-off velocity
Swim	Swim-1	4 (99)	54, 78, 201, 213	Studies that used a unique type of experimental set-up and design, i.e., these were not following one of the standard protocols in fish swimming. The number represents the repeat test order.
	Swim-2	1 (24)	54	
	Swim-3	1 (23)	54	
	Swim-4	1 (7)	54	
TTF	TTF-1	13 (1353)	2, 57, 60, 79, 84, 61, 105, 201, 213, 11, 54, 216, 217	Time to fatigue. Fish are swum at defined velocity until they reach fatigue (unable to continue swimming)
	TTF-2	3 (163)	54, 216, 217	
	TTF-3	1 (116)	217	
U_{crit}	EMG-$\mathrm{U}_{\mathrm{crit}}$	7 (21)	35, 37, 41, 62, 87, 88, 33	Critical swim speed (Brett 1964); established swim performance test in fish swimming. U_{crit} is measured in a swim tunnel or flume, where velocity is increased in increments (step test) until fish reaches fatigue. The number represents the repeat test order. EMG-$\mathrm{U}_{\mathrm{crit}}$ denote U_{crit} test performed on fish instrumented with EMG tags. The results of these test are used to calibrate EMG tags and predict swim speed in field tracking studies.
	U_{crit}-1	63 (852)	1, 3, 4, 6, 19, 7, 9, 10, 13, 14, 15, 16, 17, 28, 37, 39, 42, 43, 44, 55, 57, 65, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 80, 81, 82, 83, 84, 85, 86, 87, 89, 90, 91, 92, 93, 94, 95, 96, 100, 12, 102, 104, 105, 201, 202, 203, 204, 205, 206, 212, 215, 27, [25, 26, 48]	
	U_{crit}-2	16 (216)	19, 7, 10, 13, 14, 15, 16, 68, 69, 76, 81, 82, 90, 92, 93, [25, 26, 48]	
	U_{crit}-3	4 (14)	19, 69, 90, 93	
	U_{crit}-4	2 (4)	69, 93	
U_{max}	U_{max}	4 (158)	18, 24, 45, 76	Constant acceleration test; established swim performance test in fish swimming. U_{max} is measured in a swim tunnel or flume, where velocity is increased continuously at a defined rate until fish reaches fatigue. The number represents the repeat test order. This is sometimes reported as U_{cat} for constant acceleration test.

Note: The table contains the main category (the largest grouping that was used for analysis and data presentation), sub-categories (finer scale categories of used swim tests), sample sizes (*N*, number of studies; *n*, number of entries in database), the reference number of all corresponding studies, and description of the categories. Ref. ID, Reference ID number; the matched reference list is provided at the end of the Appendix B.

sub-categories. The intrinsic fish conditions that were noted from the literature were subset in 12 sub-categories: “diet“, ”exercise trained“, “density,” “density, exercise trained,” ”fallback“, ”infection“, ”mature“, ”pass“, ”prior anesthetic“, ”spawned“, ”toxicant “, and ”unhealthy“. Similarly, also extrinsic swim conditions that define the swimming environment were extracted when possible and were subset in 7 sub-categories: ”Dam“, ”Fall“, ”Fraser River“, ”Klickitat River“, ”other“, ”Shibetsu River“, and ”Toyohira River". The main intrinsic and extrinsic conditions that were noted and their classification in the corresponding subcategories are detailed in Tables A5 and A6.

Sex, male or female, was noted when available. Sex was denoted as “mixed” for entries reporting swim speeds of pooled sexes or for entries when the sex was not specified. One exception of sex classification was allowed when the sex distribution for a group of fish was noted 93% female, which we denoted as female for the entry (reference [1; Brett 1965*a*; Appendix B]). Further, the salinity of the water during swim was noted in one of the three categorical groups, saltwa-

Table A5. The summary of swim (extrinsic) conditions defined in the data.

Condition	Subcategory of the condition	*N* (*n*)	Ref. ID	Description
Dam	American-Dam	1 (8)	87	A set of conditions in American River, CA, USA within a section with dam.
	Columbia-Dam	1 (8)	35	A set of conditions in Columbia River, WA, USA within a section with dam.
	Fraser-Dam	2 (16)	22, 23	A set of conditions in Fraser River, BC, Canada within a section with dam.
Fall	Fall-artificial	2 (9)	40, 58	Artificial fall conditions that were used to measure swim performance of salmon during simulated passage
Fraser	Fraser-Difficult	1 (4)	47	Author defined segment in Fraser River, BC, Canada. Swim speeds were recorded for each section. Segment # 1 (Segm-1) includes The Hell's Gate
	Fraser-Easy	1 (4)	47	
	Fraser-Intermediate	1 (4)	47	
	Fraser-Segm1	1 (13)	29	
	Fraser-Segm10	1 (11)	29	
	Fraser-Segm2	3 (22)	20, 21, 29	
	Fraser-Segm3	1 (15)	29	
	Fraser-Segm4	3 (22)	20, 21, 29	
	Fraser-Segm5	1 (12)	29	
	Fraser-Segm6	1 (13)	29	
	Fraser-Segm7	2 (17)	21, 29	
	Fraser-Segm8	1 (11)	29	
	Fraser-Segm9	3 (18)	20, 21, 29	
Klickitat	Klickitat-Falls	1 (37)	36	Natural fall conditions in Klickitat River, WA, USA
other	Ammonia	1 (1)	72	Elevated water ammonia levels
	hypoxia	1 (4)	19	Environmental hypoxia (13.3–18.8 kPa)
	pH 5.15	1 (2)	71	Lower pH in the water
	pH 5.24 + Al	1 (2)	71	Lower pH and Al presence in the water
Shibetsu	Shibetsu-Construction	2 (26)	39, 88	Section in Shibetsu River, Japan that was modified by constructions (either reconstructed or canalized)
Toyohira	Toyohira-GroundSill	2 (12)	41, 44	A set of conditions in Toyohira River, Japan. Section with a groundsill.
	Toyohira-Segm1	1 (4)	44	
	Toyohira-Segm2	1 (4)	44	
	Toyohira-Segm3	1 (4)	44	
	Toyohira-Segm4	1 (4)	44	
	Toyohira-Segm5	1 (4)	44	
	Toyohira-Segm6	1 (4)	44	
	Toyohira-Segm7	1 (4)	44	
	Toyohira-Segm8	1 (4)	44	
NA	N = 91 (3200)		1, 2, 3, 4, 5, 6, 19, 7, 8, 9, 10, 13, 14, 15, 16, 18, 17, 24, 28, 30, 31, 37, 38, 39, 41, 42, 43, 44, 45, 46, 50, 54, 55, 56, 57, 60, 62, 63, 65, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 61, 90, 33, 91, 92, 93, 94, 95, 96, 100, 12, 102, 104, 105, 201, 202, 203, 204, 205, 206, 53, 212, 213, 215, 214, 11, 216, 217, 27, [25, 26, 48]	

Notes: The table contains the main category (the largest grouping that was used for analysis and data presentation), sub-categories (finer scale categories that described extrinsic conditions in each study), sample sizes (*N*, number of studies; *n*, number of entries in database), the reference number of all corresponding studies, and description of the categories. NA, not available; this includes all studies that did not have any of the classifications. Ref. ID, Reference ID number; the matched reference list is provided at the end of the Appendix B.

ter (SW, $>$ 25 ppt), freshwater (FW, 0 ppt) or brackish water (SW/FW < 25 ppt and $>$ 0 ppt).

Additional variables that were sparsely reported in the literature, but that can affect swimming ability of fish were extracted when possible. These were grouped as follows: (i) *surgery or instrumentation*: in the laboratory most of the surgery is performed to measure cardiovascular performance of salmon while swimming, in the field (tracking studies) fish are instrumented with electromyogram tags (EMG tags), tri-axial accelerometers, magnetic ring, radio tags, and acoustic tags (insertion of PIT, passive integrated transponder, tags were not classified as surgery) (Table A7); (ii) *quantitative measures of maturity:* gonad weight (g) or GSI (gonad weight/body weight); (iii) *water flow velocity* $(\mathrm{cm \cdot s^{-1}})$ *and/or discharge* $(\mathrm{cm^3 \cdot s^{-1}})$ in field studies; (iv) *mortality,* which we included as a binomial variable (1 $=$ mortality reported, 0 $=$ mortality not mentioned, not reported), with general assumption regarding field studies where fish that were not successful mi-

Table A6. The summary of fish (intrinsic) conditions defined in the data.

Condition	*N studies (n entries)*	Ref. ID	Description
Anemia	1 (19)	206	Fish with reduced number of red blood cells
Density	1 (2)	94	Fish reared at varying densities (high, and low)
Density Exercise Trained	1 (2)	94	Fish reared at varying densities and at high flow
Diet	2 (18)	81, 82	Fish fed different types of diets
Exercise Trained	2 (9)	73, 75	Fish undergone exercise training
Fallback	4 (18)	8, 36, 38, 41	Fish reported as non-successful migrants in the field studies
Fasted	1 (48)	203	Fish at fasted state
Infection	6 (25)	13, 15, 55, 93, 96, 54	Fish prone to infection or fish that were infected at different severity levels (prone to fungal infection, weak *Parvicapsula minibirnis* infection, strong *Parvicapsula minibirnis* infection, Sea lice infected 0.02 sealice/g, Sea lice infected 0.13 sea lice/g, *Aeromonas salmonicida*, infection, Sea lice infected 0.13 sea lice/g)
Injured	1 (16)	54	Fish with noted injury
Kelts	2 (30)	201, 202	Lifestage in Atlantic salmon, mature fish, that kad spawned and are returning to the ocean again
Mature	13 (220)	6, 13, 22, 23, 56, 71, 83, 89, 61, 201, 214, 54, 217	Mature fish. * different terms were used to describe maturity of fish. The subcategory list here represents more common ways, but not all. (gravid, spawning, nearing spawning condition, ripe within days of spawning, At terminal spawning ground, mature, mature; pre stripping near/at spawning)
Pass	4 (17)	8, 36, 38, 41	Fish reported as successful migrants in the field studies
Polycythemia	1 (35)	206	Fish with elevated number of red blood cells
Prior anesthetic	2 (10)	42, 77	Fish that had undergone anesthesia near before swimming
Spawned	1 (2)	6	Fish that had spawned
Toxicant	3 (9)	19, 7, 72	Fish exposed to a toxin prior swimming. DHA, dehydroabietic acid; PCP, pentachlorophenol; sublethal levels of Ammonia
Unhealthy	3 (59)	7, 14, 18, 217	Fish in unhealthy conditions
NA	85 (2984)	1, 2, 3, 4, 5, 19, 7, 9, 10, 13, 15, 16, 18, 17, 20, 21, 24, 28, 29, 30, 31, 35, 37, 39, 41, 42, 43, 44, 45, 47, 46, 50, 54, 55, 57, 40, 58, 60, 62, 63, 65, 36, 68, 69, 70, 72, 73, 74, 75, 76, 77, 78, 79, 80, 84, 85, 86, 87, 88, 90, 33, 91, 92, 93, 95, 96, 100, 12, 102, 104, 105, 201, 203, 204, 205, 206, 53, 212, 213, 215, 11, 216, 27, [25, 26, 48], 217	

Notes: The table contains the main category (the largest grouping that was used for analysis and data presentation), sub-categories (finer scale categories that described intrinsic conditions in each study), sample sizes (*N*, number of studies; *n*, number of entries in database), the reference number of all corresponding studies, and description of the categories. NA, not available; this includes all studies that did not have any of the classifications. Ref. ID, Reference ID number; the matched reference list is provided in Appendix B.

grants were denoted positive for mortality, unless otherwise specified by author; and lastly (v) *tracking study*, which was included as a binomial variable (1 or 0), where 1 denotes tracking study where swim speed is measured under field conditions as adult salmon are completing a part of their spawning migration, and 0 denotes controlled (laboratory) study. We caution making meta-analytical inference about how these factors influence swimming ability in adult salmon because the data are very coarse in each sub-category.

Data analysis

All analyses were performed in R 3.5.1 (2018). The sample size of complete data entries was insufficient to robustly estimate how swim capacity differs intra- and inter-specifically and across environmental conditions. For instance, entry of mean swim speed of a group of fish did not have a corresponding body size measurement (length or mass), or the swim speed would be only reported in relative units, body lengths per second (relative swim speed, BL/s). To populate a

Table A7. The summary of categories tagging methods defined in the data.

Condition	*N studies (n entries)*	Ref. ID	Description
Accelerometer	4 (30)	22, 23, 47, 27	Surgically implanted acceleration transmitter used for field tracking.
AcousticTag	1 (8)	46	Surgically implanted sound wave emitting tag used for field tracking.
Cannulation	13 (93)	19, 7, 15, 16, 17, 68, 72, 74, 76, 79, 80, 206, 212	A surgical procedure where cannula is placed inside the aorta to provide access to blood. Both dorsal and ventral aorta cannulation was reported.
Cannulation and FlowProbe	4 (200)	95, 205, 206, [25, 26, 48]	Both procedures, cannulation and insertion of blood flow probe, were performed.
DST-centi-HR-ACT bio-logger	1 (1)	100	An instrumentation with implantable leadless heart rate, activity, and temperature logger.
DST-HR bio-logger	1 (13)	102	
EMGtag	23 (401)	5, 8, 20, 21, 29, 36, 35, 37, 38, 39, 41, 42, 43, 44, 57, 62, 65, 69, 70, 87, 88, 33, 201	Electromyogram tag. Surgically implanted tag with electrodes directly inserted in red and/or white muscle to measure muscular activity.
FlowProbe	3 (69)	24, 83, 96	A surgical instrumentation of blood flow probes around the dorsal aorta.
Ligation	2 (3)	4, 73	A surgical procedure of closing off coronary artery.
MagneticRing	1 (2)	63	An instrumentation with a magnetic ring for field tracking, tag is attached to the body of fish.
Optode implant	1 (4)	92	Implantation of a sensor into the sinus venosus of the heart
RadioTag	2 (21)	56, 60	An instrumentation with radio transmitter, tag is attached to the body of fish.
NA	$N = 66$ (2678)	1, 2, 3, 4, 6, 9, 10, 13, 14, 18, 24, 28, 30, 31, 37, 39, 41, 42, 44, 45, 50, 54, 55, 57, 40, 58, 60, 65, 69, 70, 71, 73, 75, 76, 77, 78, 81, 82, 84, 85, 86, 87, 89, 61, 90, 91, 93, 94, 12, 102, 53, 213, 215, 214, 11, 216, 217, 27, [25, 26, 48], 102, 104, 105, 201, 202, 203, 204	

database with absolute swim speed (cm/s) entries, we used the reported length (cm) of the fish and calculated absolute swim speed = relative swim speed × BL (Fig. S1). When BL was not reported, but body mass was, we used a weight–length relationship $W = a \times \mathrm{BL}^b$ (Jones et al. 1999) to estimate the BL; in this equation W = body mass, BL = body length, a and b are accepted species-level estimates in many fish species from a linearized form of this equation: log(W) = log(a) + log(BL), where a is the intercept and b is the slope of the regression. The, the estimated body length was used to calculate the absolute swim speed. The used coefficients (a and b) for each species, the comparison between the reported absolute swim speed and estimated absolute swim speed when available are available in Supplementary Fig. S1.

APPENDIX B

Reference list of studies collated for this review.

Ref ID	Reference
1	Brett, J.R. 1965. The relation of size to rate of oxygen and sustained swimming speed of sockeye salmon (*Oncorhychus nerka*). Journal of Fisheries Research Board of Canada **22**(6): 1491–1500.
2	Brett, J.R. 1973. Energy Expenditure of Sockeye Salmon, *Oncorhynchus nerka*, During Sustained Performance. Journal of the Fisheries Research Board of Canada **30**(12): 1799–1809. doi:10.1139/f73-290.
3	Brett, J.R., and Glass, N.R. 1973. Metabolic Rates and Critical Swimming Speeds of Sockeye Salmon (*Oncorhynchus nerka*) in Relation to Size and Temperature. Journal of the Fisheries Research Board of Canada **30**(3): 379–387. doi:10.1139/f73-068.
4	Farrell, A.P., and Steffensen, J.F. 1987. Coronary ligation reduces maximum sustained swimming speed in Chinook salmon, *Oncorhynchus tshawytscha*. Comparative Biochemistry and Physiology Part A **87**(1): 35–37.
5	Quinn, T.P. 1988. Estimated swimming speeds of migrating adult sockeye salmon. Canadian Journal of Zoology **66**(10): 2160–2163. doi:10.1139/z88-322.
6	Williams, I.V., and Brett, J.R. 1987. Critical Swimming Speed of Fraser and Thompson River Pink Salmon (*Oncorhynchus gorbuscha*). Canadian Journal of Fisheries and Aquatic Sciences **44**(2): 348–356. doi:10.1139/f87-043.
7	Jain, K.E., Birtwell, I.K., and Farrell, A.P. 1998. Repeat swimming performance of mature sockeye salmon following a brief recovery period: a proposed measure of fish health and water quality. **76**: 1488–1496.
8	Hinch, S.G., and Bratty, J. 2000. Effects of Swim Speed and Activity Pattern on Success of Adult Sockeye Salmon Migration through an Area of Difficult Passage. Transactions of the American Fisheries Society **129**: 598–606.
9	MacNutt, M.J., Hinch, S.G., Lee, C.G., Phibbs, J.R., Lotto, A.G., Healey, M.C., and Farrell, A.P. 2006. Temperature effects on swimming performance, energetics, and aerobic capacities of mature adult pink salmon (*Oncorhynchus gorbuscha*) compared with those of sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Zoology **84**(1): 88–97. doi:10.1139/z05-181.
10	Lee, C.G., Devlin, R.H., and Farrell, A.P. 2003. Swimming performance, oxygen consumption and excess post-exercise oxygen consumption in adult transgenic and ocean-ranched coho salmon. Journal of Fish Biology **62**(4): 753–766. doi:10.1046/j.1095-8649.2003.00057.x.
11	Brett, J.R. 1967. Swimming Performance of Sockeye Salmon (*Oncorhynchus nerka*) in relation to Fatigue Time and Temperature. J. Fish. Res. Bd. Can. **24**(8): 1731–1741. doi:10.1139/f67-142.
12	Lee, C.G., Farrell, A.P., Lotto, A., MacNutt, M.J., Hinch, S.G., and Healey, M.C. 2003. The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. Journal of Experimental Biology **206**(18): 3239–3251. doi:10.1242/jeb.00547.
13	Farrell, A.P., Lee, C.G., Tierney, K., Hodaly, A., Clutterham, S., Healey, M., Hinch, S., and Lotto, A. 2003. Field-based measurements of oxygen uptake and swimming performance with adult Pacific salmon using a mobile respirometer swim tunnel. Journal of Fish Biology **62**(1): 64–84. doi:10.1046/j.1095-8649.2003.00010.x.
14	Tierney, K.B., and Farrell, A.P. 2004. The relationships between fish health, metabolic rate, swimming performance and recovery in return-run sockeye salmon, *Oncorhynchus nerka* (Walbaum). Journal of Fish Diseases **27**(11): 663–671. doi:10.1111/j.1365-2761.2004.00590.x.
15	Wagner, G.N., Hinch, S.G., Kuchel, L.J., Lotto, A., Jones, S.R., Patterson, D.A., Macdonald, J.S., Kraak, G.V.D., Shrimpton, M., English, K.K., Larsson, S., Cooke, S.J., Healey, M.C., and Farrell, A.P. 2005. Metabolic rates and swimming performance of adult Fraser River sockeye salmon (*Oncorhynchus nerka*) after a controlled infection with *Parvicapsula minibicornis*. Canadian Journal of Fisheries and Aquatic Sciences **62**(9): 2124–2133. doi:10.1139/f05-126.
16	Wagner, G.N., Kuchel, L.J., Lotto, A., Patterson, D.A., Shrimpton, J.M., Hinch, S.G., and Farrell, A.P. 2006. Routine and Active Metabolic Rates of Migrating Adult Wild Sockeye Salmon (*Oncorhynchus nerka* Walbaum) in Seawater and Freshwater. Physiological and Biochemical Zoology **79**(1): 100–108. doi:10.1086/498186.
17	Cech, J.J., McEnroe, M., and Randall, D.J. 2004. Coho salmon haematological, metabolic and acid-base changes during exercise and recovery in sea water. Journal of Fish Biology **65**(5): 1223–1232. doi:10.1111/j.0022-1112.2004.00489.x.
18	Farrell, A.P., Gallaugher, P.E., Fraser, J., Pike, D., Bowering, P., Hadwin, A.K.M., Parkhouse, W., and Routledge, R. 2001. Successful recovery of the physiological status of coho salmon on board a commercial gillnet vessel by means of a newly designed revival box. Canadian Journal of Fisheries and Aquatic Sciences **58**(10): 1932–1946. doi:10.1139/cjfas-58-10-1932.
19	Farrell, A.P., Gamperl, A.K., and Birtwell, I.K. 1998. Prolonged swimming, recovery and repeat swimming performance of mature sockeye salmon *Oncorhychus nerka* exposed to moderate hypoxia and pentacholorophenol. Journal of Experimental Biology **201**: 2183–2193.
20	Standen, E.M., Hinch, S.G., Healey, M.C., and Farrell, A.P. 2002. Energetic costs of migration through the Fraser River Canyon, British Columbia, in adult pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) salmon as assessed by EMG telemetry. Canadian Journal of Fisheries and Aquatic Sciences **59**(11): 1809–1818. doi:10.1139/f02-151.
21	Hinch, S.G., Standen, E.M., Healey, M.C., and Farrell, A.P. 2002. Swimming patterns and behaviour of upriver-migrating adult pink (*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon as assessed by EMG telemetry in the Fraser River, British Columbia, Canada. Hydrobiologia **483**: 147–160. doi:10.1007/978-94-017-0771-8_17.

(*continued*).

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