

Oxygen uptake in Pacific salmon *Oncorhynchus* spp.: when ecology and physiology meet

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Over the past several decades, a substantial amount of research has examined how cardiorespiratory physiology supports the diverse activities performed throughout the life cycle of Pacific salmon, genus *Oncorhynchus*. Pioneering experiments emphasized the importance of aerobic scope in setting the functional thermal tolerance for activity in fishes. Variation in routine metabolism can have important performance and fitness consequences as it is related to dominance, aggression, boldness, territoriality, growth rate, postprandial oxygen consumption, life history, season, time of day, availability of shelter and social interactions. Wild fishes must perform many activities simultaneously (*e.g.* swim, obtain prey, avoid predators, compete, digest and reproduce) and oxygen delivery is allocated among competing organ systems according to the capacity of the heart to deliver blood. For example, salmonids that are simultaneously swimming and digesting trade-off maximum swimming performance in order to support the oxygen demands of digestion. As adult Pacific salmonids cease feeding in the ocean prior to their home migration, endogenous energy reserves and cardiac capacity are primarily partitioned among the demands for swimming upriver, sexual maturation and spawning behaviours. Furthermore, the upriver spawning migration is under strong selection pressure, given that Pacific salmonids are semelparous (single opportunity to spawn). Consequently, these fishes optimize energy expenditures in a number of ways: strong homing, precise migration timing, choosing forward-assist current paths and exploiting the boundary layer to avoid the strong currents in the middle of the river, using energetically efficient swimming speeds, and recovering rapidly from anaerobic swimming. Upon arrival at the spawning ground, remaining energy can be strategically allocated to the various spawning behaviours. Strong fidelity to natal streams has resulted in reproductively isolated populations that appear to be locally adapted physiologically to their specific environmental conditions. Populations with more challenging migrations have enhanced cardiorespiratory performance. Pacific salmonids are able to maintain aerobic scope across the broad range of temperatures encountered historically during their migration; however, climate change-induced river warming has created lethal conditions for many populations, raising conservation concerns. Despite considerable research examining cardiorespiratory physiology in Pacific salmonids over the last 70 years, critical knowledge gaps are identified.

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Key words: aerobic scope; energetics; local adaptation; migration; oxygen consumption; temperature.

INTRODUCTION

Fish ecology and fish physiology represent a division of labour to understand the interactions and mechanisms of nearly 50% of the vertebrate animals living on this planet. Knowledge of oxygen uptake in fishes has reached a point that

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physiological mechanisms may be related with ecology. Indeed, there is such a wealth of physiological and ecological information for Pacific salmon *Oncorhynchus* spp. that it has even been significant for fisheries management. The present overview is not meant to be prescriptive or a comprehensive literature review, but rather it illustrates how physiology and ecology have been successfully fused (with fisheries management in mind) for one group of fishes and one physiological function (the delivery of oxygen to tissues). The emphasis on thermal effects is deliberate, this is where there is a great deal of new knowledge which finds important traction in an era of global climate change. Knowledge gaps certainly remain and these are pointed out, as a need for further research and to show that other factors still need to be considered.

AN INTRODUCTION TO PACIFIC SALMON LIFE HISTORY

The west coast of North America is home to six species of anadromous Pacific salmon: sockeye salmon *Oncorhynchus nerka* (Walbaum 1792), Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792), coho salmon *Oncorhynchus kisutch* (Walbaum 1792), pink salmon *Oncorhynchus gorbuscha* (Walbaum 1792), chum salmon *Oncorhynchus keta* (Walbaum 1792) and steelhead trout *Oncorhynchus mykiss* (Walbaum 1792). While they share a common overall life history, the details vary widely among species and populations; a comprehensive overview is given by Groot & Margolis (1991). All six species start their life in fresh water, migrate to sea to feed and grow and eventually return to their natal streams to spawn. With the exception of *O. mykiss*, Pacific salmonids have a single opportunity to reproduce because they die after spawning (semelparity). Adults cease feeding in the ocean prior to returning to their spawning grounds, which means that they must rely on endogenous energy stores to fuel the primary activities that remain in their life, *i.e.* upriver swimming to natal spawning areas, ongoing reproductive maturation and the final spawning event. These species are renowned for an exceptional homing ability, being able to locate their natal spawning area after a migration of many thousands of km across the ocean. This strong fidelity has resulted in many genetically and geographically distinct populations of a given species within a single catchment (Beacham *et al.*, 2005). As a result, there is an increased potential for physiological traits to be geographically segregated among populations.

Eggs are typically deposited in the substratum of freshwater lakes or streams in the autumn, with hatching usually occurring in the winter or spring. The alevins remain under gravel, nutritionally supported by their yolks sac and emerge as fry 4–6 weeks later to begin feeding. Shortly thereafter, some species and populations head to sea (*e.g.* *O. gorbuscha* and *O. keta*, some populations of *O. tshawytscha* and *O. nerka*), while others spend 1–2 years in freshwater streams or lakes as parr, growing to a much larger size before embarking on their out-migration as smolts in the spring (*e.g.* most *O. nerka*, *O. kisutch* and *O. tshawytscha*). Adults forage and grow in the ocean for 1–6 years, reaching *c.* 2 kg (*e.g.* *O. gorbuscha*) to >45 kg in some cases (*e.g.* *O. tshawytscha*). The return spawning migration can be truly spectacular, with some populations travelling over 1000 km in fresh water to reach distant, interior spawning grounds. Millions of fishes can spawn in a stretch of river spanning just a few km during a single 3–4 week period. *Oncorhynchus mykiss* are an interesting study species because a single population can comprise both the anadromous form

(steelhead trout) and freshwater residents (rainbow trout) that can interbreed and produce offspring capable of adopting either life-history strategy.

Pacific salmonids encounter widely different habitats and anthropogenic influences across their North American range, which extends from California to Alaska. For example, populations returning to Bristol Bay, Alaska, encounter relatively pristine rivers and lakes, whereas many of their endangered counterparts in the Sacramento River, California, must cope with extensive habitat degradation. Even within a single catchment, species and populations may experience considerable differences in their environment (*e.g.* migration distance, elevation, temperature, river flow, hydrological barriers, oxygen tension, predators, fishing pressure, prey density and type). Indeed, populations are hypothesized to be locally adapted to their specific environmental conditions (Taylor, 1991; Eliason *et al.*, 2011; Fraser *et al.*, 2011). Overall, this remarkable natural diversity and complex life history make them a fascinating model to examine the intersection of physiology and ecology, especially with respect to oxygen delivery to tissues.

The cardiorespiratory system must deliver sufficient oxygen to support the cellular respiration required for the daily metabolic activities of wild Pacific salmonids such as ascending rapids, escaping predators, foraging, digesting, growing, sexually maturing, competing for mates and territory. This review focuses on research in North America with an emphasis on the freshwater phase as little is known about the marine phase of the life cycle. Occasionally, studies on other salmonids [*e.g.* Atlantic salmon *Salmo salar* L. 1758, brown trout *Salmo trutta* L. 1758 and brook trout *Salvelinus fontinalis* (Mitchill 1814)] are included in this review if a similar ecology and life history permits a logical extrapolation. The first section details the energetic demands of baseline metabolism and three essential life functions (locomotion, digestion and reproduction). The second section examines how temperature and local adaptation influence cardiorespiratory physiology. The final section explores the management and conservation implications of this research and concludes with future research directions.

PIONEERS OF SALMONID CARDIORESPIRATORY PHYSIOLOGY

Salmonid cardiorespiratory physiology research was pioneered by Fry (1947, 1948, 1957, 1971), Brett (1952, 1964, 1965, 1967, 1971*a, b*), Brett *et al.* (1958) and Brett & Glass (1973). Fry (1947) was interested in the effect of the environment on animal activity, classifying environmental factors as lethal, masking, directive, controlling, limiting and accessory. Much of Fry's (1947, 1948) research focused on the influence of temperature on performance across a range of species. He observed that the optimal temperature for activity can be determined by measuring the relationship of standard and active metabolic rate (AMR) with temperature and calculating scope for activity [the difference between AMR and standard metabolic rate (SMR) (Fry, 1947); now commonly referred to as aerobic scope (Fig. 1)]. This insightful observation has spawned an entire field of study that is relevant to research into global climate change (Pörtner & Knust, 2007; Nilsson *et al.*, 2009) and the theory upon which the oxygen- and capacity-limited thermal tolerance hypothesis is founded (Pörtner, 2001; Pörtner & Farrell, 2008). Building upon Fry's classic studies, Brett systematically assessed the energetics of Pacific salmonids (especially *O. nerka*) with respect to fish size, feeding, activity and temperature (Brett, 1952, 1965, 1967, 1971*a, b*; Brett & Glass, 1973).

Similarly, the works of Elliott (1982, 1991) on salmonids in Europe followed the same conceptual approach.

Other contributions to this special issue deal more fully with the measurement techniques and terminology related to oxygen consumption ($\dot{M}O_2$), therefore the following point can be brief. Tissue metabolic rate (*i.e.* heat output) is difficult to directly measure in fishes, so researchers typically measure whole animal $\dot{M}O_2$ as an indirect estimate of whole animal metabolic rate. In a laboratory setting, $\dot{M}O_2$ of fishes is measured in a respirometer as the slope of the decrease in O_2 content in the water over time (Nelson, 2016; Svendsen *et al.*, 2016). $\dot{M}O_2$ cannot be directly measured in fishes in their natural environment, and so researchers frequently use other indirect estimates of metabolic rate. Those used for salmonid research include: (1) whole body energy content at different time points during a migration (Gilhousen, 1980; Crossin *et al.*, 2004), (2) tail-beat frequency (Puckett & Dill, 1985), (3) electromyogram (EMG) biotelemetry (Geist *et al.*, 2003), (4) heart rate (electrocardiogram, ECG) biologging (Clark *et al.*, 2009), (5) accelerometry biotelemetry (Burnett *et al.*, 2014) and (6) opercular movements (Millidine *et al.*, 2009a). These indirect techniques, however, need to be calibrated back to caloric or $\dot{M}O_2$ equivalents to maximize their usefulness.

STANDARD AND ROUTINE METABOLISM

The minimum amount of energy required to maintain basic physiological function (*e.g.* maintain ion gradients, protein turnover and cardiac performance) is termed the SMR in ectotherms. In practice, it is difficult to determine SMR in wild fishes since by definition $\dot{M}O_2$ must be measured over several days in an inactive, post-absorptive, non-reproducing fishes (Chabot *et al.*, 2016). Thus, resting or routine metabolic rate (RMR) is a more pragmatic measure that is frequently reported. RMR is generally the lowest recording of $\dot{M}O_2$ as permitted by the experimental setting and can include low but minimal levels of spontaneous activity.

Standard and routine metabolism has important ecological implications for fishes. Within a species, RMR can vary widely among individuals even after accounting for fish size, age and temperature (Enders & Scruton, 2005; Tyler & Bolduc, 2008). Moreover, an individual's RMR is repeatable over time (McCarthy, 2000; Seppänen *et al.*, 2010). SMR and RMR have been positively correlated with dominance, aggression, boldness, territoriality and growth rate in *S. salar*, *S. trutta* and *O. mykiss* (Metcalf *et al.*, 1995; Cutts *et al.*, 1998; Álvarez & Nicieza, 2005; Reid *et al.*, 2012; Sloat & Reeves, 2014). This variation has important implications for performance and fitness because only surplus energy above SMR can be used for reproduction, growth and activity. In addition, SMR can take up a large proportion of a fish's total energy budget (Secor, 2009) and trade-offs exist between a cost-minimizing *v.* energy maximizing strategy. For example, elevated SMR was positively correlated with peak postprandial $\dot{M}O_2$ and the magnitude of postprandial $\dot{M}O_2$ in *S. salar* (Millidine *et al.*, 2009b), which could allow for a superior growth potential *via* enhanced extraction and assimilation of nutrients from a given meal. Thus, in favourable environments with a surplus of food, individual fish with high SMR could have a greater potential for fast growth. When food becomes limiting or unpredictable, however, individuals with a low SMR may have the advantage.

Individual variation in energy metabolism has been shown to influence life history of *O. mykiss*. Specifically, high SMR increased the rate of anadromy in females but not in

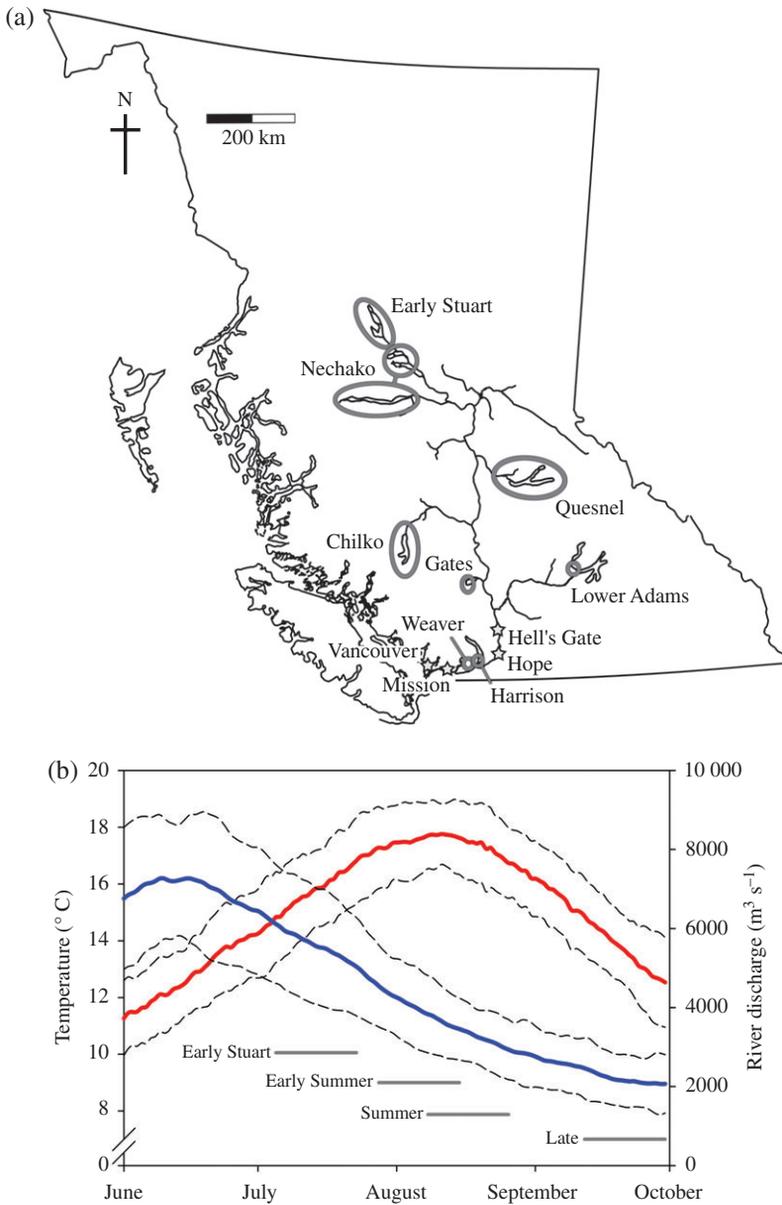


FIG. 1. (a) Map of the Fraser River catchment, British Columbia, Canada. Spawning areas for eight *Oncorhynchus nerka* populations are indicated. (b) Mean temperature (—) and mean discharge (—) of the Fraser River at Hell's Gate for June to September from 1941 to 2006. ---, s.d. Managers group the various Fraser River *O. nerka* populations into four major run timing groups based on when they enter the river. —, the historic 19 day peak period of passage through Hell's Gate for the four major run timings for *O. nerka*: Early Stuart (median date = 14 July), Early Summer (e.g. Gates, median date = 6 August), Summer (e.g. Chilko, Nechako, Quesnel, median date = 17 August), Late (e.g. Lower Adams, median date = 21 September). Note that Weaver Creek and Harrison populations do not pass through Hell's Gate but are part of the Late Run group.

males from one population of *O. mykiss* (Sloat & Reeves, 2014). The authors suggested that fish with high SMR (and thus elevated metabolic costs for maintenance of basic functions) have proportionally less surplus energy and are energetically constrained from freshwater maturation and compensate by undertaking a marine feeding migration (Sloat & Reeves, 2014).

Standard and routine metabolism is also known to be time and context specific. For example, fishes exhibit diurnal rhythms and accordingly $\dot{M}O_2$ varies considerably throughout the day (Brett & Zala, 1975; Steffensen, 1989; Briggs & Post, 1997). Field metabolic rates also vary seasonally and are strongly dependent on temperature (Briggs & Post, 1997). Higher feed consumption can increase SMR in juvenile *O. kisutch* and *O. mykiss*, independent of the oxygen cost of digestion, whereas starvation can decrease SMR (Van Leeuwen *et al.*, 2011, 2012). In addition, the presence of shelter is known to reduce SMR in juvenile *S. salar* (Millidine *et al.*, 2006), presumably because the physiological costs of increased vigilance against predation can be reduced. Social interactions also influence SMR and RMR. For example, juvenile *S. salar* exposed to a smaller conspecific decreased RMR by 40% while exposure to a larger fish resulted in a doubling of RMR (Millidine *et al.*, 2009a). Similarly, social stress greatly increased SMR in subordinate *S. trutta*, imposing a metabolic disadvantage (Sloman *et al.*, 2000). Consequently, all factors influencing basal and routine metabolic costs can have profound downstream effects on the total energy budget and energy utilization of the fish.

RMR has been measured in several species of sexually maturing, wild adult Pacific salmonids with the primary intent of assessing aerobic scope (Table I). These RMR estimates are higher than SMR as the oxygen cost of gonad development and restlessness in the respirometer cannot be differentiated. Accordingly, while maximum aerobic scope has probably been underestimated, the measurements that are available probably reflect the aerobic scope that is actually available beyond the costs of on-going sexual maturation.

LOCOMOTION

Across all life stages, Pacific salmonids face a diverse set of tasks that require locomotion. Aerobic swimming is used for prolonged periods of time such as when fishes migrate to new areas, forage for food and maintain position in currents. Anaerobic burst swimming is also widely used (to escape predators, obtain prey, ascend rapids and waterfalls, excavate redds and combat competitors for access to mates and territory), which makes both modes of swimming absolutely critical for evolutionary success. Accordingly, Pacific salmonids are not optimized for one form of swimming over another but, instead, have a morphology and physiology that enables them to meet both aerobic and anaerobic demands (Brett, 1995; Webb, 1995).

During aerobic swimming, $\dot{M}O_2$ can increase three to five-fold from resting levels to meet the increased tissue oxygen demand of locomotion (Norin & Clark, 2016). Sustained swimming is the primary mode of locomotion during migration, which requires a steady supply of oxygen to support oxidative phosphorylation. Indeed, Pacific salmonids can travel 20–40 km per day during their upriver spawning migration (English *et al.*, 2005). AMR is typically measured *via* a critical swimming velocity (U_{crit}) test. AMR values vary between 156 and 719 $\mu\text{mol O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ among wild adult salmonid species (Table I).

TABLE I. Routine metabolic rate (RMR, R_M), active metabolic rate (AMR, R_A) and aerobic scope for adult *Oncorhynchus* spp. Temperature range of measurements ($^{\circ}$ C) are shown in parentheses

	Oxygen consumption ($\mu\text{mol kg}^{-1} \text{min}^{-1}$)		
	R_M	R_A	Aerobic scope
<i>Oncorhynchus kisutch</i> ^{a,b,c}	69–91 (5–11)	279–395 (5–11)	195–304 (5–11)
<i>Oncorhynchus tshawytscha</i> ^{d,e,f}	62–272 (8–25)	156–355 (8–20)	120–277 (8–20)
<i>Oncorhynchus gorbuscha</i> ^{a,g,h,i}	34–191 (8–24)	284–719 (8–28)	155–531 (8–24)
<i>Oncorhynchus nerka</i>			
*Vancouver Island ^{a,j,k,l,m}	60–152 (15–21)	213–355 (5–21)	87–295 (15–21)
†Fraser River Coastal ^{a,c,n,o}	47–163 (8–24)	253–384 (8–24)	113–291 (8–24)
‡Fraser River Intermediate ^{c,p,q}	56–136 (14–20)	393–473 (14–20)	282–338 (14–20)
§Fraser River Interior ^{c,h,q,r,s}	38–203 (9–26)	189–550 (9–26)	60–422 (9–26)
Unknown ^{t,u}	76–138 (13)	315–509 (13)	239–371 (13)

^aFarrell *et al.* (2003), ^bLee *et al.* (2003c), ^cLee *et al.* (2003b), ^dGeist *et al.* (2000), ^eGeist *et al.* (2003), ^fClark *et al.* (2008), ^gWilliams *et al.* (1986), ^hMacNutt *et al.* (2006), ⁱClark *et al.* (2011), ^jBrett (1965), ^kBrett & Glass (1973), ^lFarrell *et al.* (1998), ^mJain *et al.* (1998), ⁿHinch *et al.* (1996), ^oEliason *et al.* (2013c), ^pSteinhausen *et al.* (2008), ^qEliason *et al.* (2011), ^rEliason *et al.* (2013b), ^sEliason *et al.* (2013a), ^tWagner *et al.* (2005), ^uWagner *et al.* (2006).

*Vancouver Island populations: Stamp River, Great Central and Sproat Lakes (<100 km upriver migration).

†Fraser River Coastal populations: Weaver Creek, Harrison and Cultus Lake (c. 100 km upriver migration).

‡Fraser River Intermediate populations: Gates Creek and Late Shuswap (364–480 km upriver migration).

§Fraser River Interior populations: Early Stuart, Chilko, Quesnel and Nechako (642–1071 km upriver migration).

||Unknown: *O. nerka* were collected in the ocean and population origin was not determined.

Aerobic scope can be expressed as an absolute value (aerobic scope = AMR – SMR, where AMR is active metabolic rate and SMR is standard metabolic rate) or as a proportional increase (factorial aerobic scope = AMR/SMR). Absolute aerobic scope provides information about a fish's maximum capacity to increase $\dot{M}O_2$, which is most ecologically relevant as a given task has an absolute oxygen requirement. It is largely unknown, however, exactly how much aerobic scope is necessary to perform specific tasks and activities. For example, maximum aerobic scope is probably required to successfully ascend difficult portions of the upriver migration (*e.g.* through the Fraser Canyon, BC, Canada), while other activities may require much less scope for energy (*e.g.* searching for navigational cues in the ocean). Also, it is important to note that some tasks require anaerobic metabolism and thus cannot be directly quantified as a proportion of aerobic scope. On the other hand, factorial aerobic scope can be used as an indication of how energy allocation of an individual may be affected by environmental conditions (*e.g.* hypoxia and temperature). For example, following a meal,

$\dot{M}O_2$ may double, but concurrent hypoxia could reduce factorial scope to <2 , meaning there may be insufficient O_2 for normal digestion and thus lead to impaired digestive processes in a hypoxic environment (Farrell & Richards, 2009).

Burst swimming is essential for most species of fishes to escape predators, ascend difficult rapids, compete for mates or territory and obtain prey. While aerobic metabolism supports swim speeds up to 70–80% of maximum during U_{crit} tests, anaerobic metabolism is required to support swimming speeds approaching and exceeding U_{crit} (Geist *et al.*, 2003). High intensity burst swimming is powered by white muscle ($>50\%$ of body mass in Pacific salmonids) and is primarily fuelled by anaerobic metabolism, which allows for a more rapid delivery of ATP to locomotory muscles (consequently, the higher tail-beat frequency associated with burst swimming). This leads to an accumulation of lactate and H^+ ions, as well as a depletion of oxygen stores and high-energy phosphates. Anaerobic exercise comes at a cost in terms of both recovery time and energy. The energetic cost of anaerobic activity cannot be directly quantified in real time by measuring $\dot{M}O_2$ but can be estimated by measuring $\dot{M}O_2$ during recovery.

Excess post-exercise oxygen consumption (EPOC) represents the oxygen required to re-establish homeostasis after exercise (*e.g.* restore high-energy phosphates, oxygen stores, glycogen, endocrine homeostasis, ionic and osmotic balance). EPOC is typically measured in a swim tunnel respirometer by monitoring $\dot{M}O_2$ throughout recovery until it returns to resting levels. The duration of EPOC varies, depending on life stage, intensity of exercise and temperature. Following a U_{crit} swim test, EPOC lasted 4–5 h in juvenile *O. nerka* (Brett, 1964) and 42–78 min in adult *O. nerka* (Lee *et al.*, 2003a). EPOC following a simulated capture event (3 min chase with 1 min of air exposure) at 7° C lasted *c.* 9 h for jack *O. kisutch* and *c.* 12 h for full-size *O. kisutch* (Clark *et al.*, 2012). The energetic cost of EPOC following a U_{crit} swim test is not trivial, adding an estimated additional 21–51% to $\dot{M}O_{2max}$ (Lee *et al.*, 2003a), which is an important cost that has rarely been taken into account when developing energetic models (Martin *et al.*, 2015).

Rapid recovery from burst exercise and the ability to repeat swim performance are critical throughout the salmonid life cycle. For example, fry need to rapidly recover from predator attacks in order to resume normal foraging behaviours and avoid being eaten in a weaker state, whereas migrating adults need to repeatedly burst swim through rapids to ensure a timely migration. Individuals can often be observed recovering in back eddies and pools after traversing difficult barriers or after failing to traverse a difficult barrier before attempting again (Brett, 1995). Therefore, an important observation is that Pacific salmonids do not have to fully recover physiologically between repetitive swim tests (Kieffer *et al.*, 2011; Eliason *et al.*, 2013a) in order to achieve an excellent repeat swim performance (Farrell *et al.*, 1998, 2003; Jain *et al.*, 1998; Lee *et al.*, 2003b; MacNutt *et al.*, 2006; Wagner *et al.*, 2006; Eliason *et al.*, 2013a). Furthermore, moderate swimming following exhaustive exercise can improve swim performance in subsequent swimming tests in *O. mykiss* and *S. fontinalis* (Milligan *et al.*, 2000; Kieffer *et al.*, 2011), and can accelerate recovery in wild *O. kisutch* after capture with commercial fishing gear (Farrell *et al.*, 2001). The mechanisms that accelerate recovery are poorly understood, but may involve cortisol dynamics or oxygen delivery improvements (Milligan *et al.*, 2000; Kieffer *et al.*, 2011).

Adults do not feed during their upriver spawning migration, so the entire migration is supported by endogenous energy stores. As such, Pacific salmonids are hypothesized to minimize energy expenditures whenever possible (Hinch & Rand, 2000). The

energetic cost of transport (COT) is expressed as the amount of oxygen consumed per unit distance travelled (e.g. $\mu\text{mol O}_2 \text{ kg}^{-1} \text{ m}^{-1}$). COT has been traditionally reported to have U-shaped relationship with swimming velocity (i.e. COT is highest at the lowest and highest speeds, and optimal at some intermediate speed) in several species of fishes (Wakeman & Wohlschlag, 1982; Webb, 1995; Lee *et al.*, 2003a). Swimming speed has been suggested to be optimal at *c.* 1 body length (L_B) s^{-1} for most of the Pacific salmonids, including Chehalis *O. kisutch*, Weaver Creek *O. nerka* and juvenile *O. nerka* (Webb, 1995; Lee *et al.*, 2003a). COT, however, plateaued at speeds *c.* $>1 L_B \text{ s}^{-1}$ for *O. nerka* populations with more challenging migrations [Gates Creek, Chilko, Early Stuart and Quesnel (Lee *et al.*, 2003b; Eliason *et al.*, 2013a)], indicating that some populations can maintain a low COT over a broad range of swimming speeds. Thus, the metabolically optimal range of swim speeds for salmonids with challenging migrations is probably between *c.* $1 L_B \text{ s}^{-1}$ and *c.* 70–80% of U_{crit} [e.g. 80% of $U_{\text{crit}} = c. 1.9 L_B \text{ s}^{-1}$ for Early Stuart *O. nerka* (Eliason *et al.*, 2013a)].

There are two potential confounding factors when considering COT. Once fish reach speeds exceeding their aerobic swimming capacity and start to recruit anaerobic fibres to fuel swimming, COT is underestimated if it does not account for EPOC. A second confounding factor involves environmental temperature because SMR varies with temperature and this has a consequence to COT. Therefore, net COT (the amount of oxygen consumed per unit distance travelled after SMR has been subtracted from active MO_2) is a more useful term when comparing the cost of locomotion at different temperatures (Lee *et al.*, 2003a; Eliason *et al.*, 2013b). Net COT eliminates a variable SMR from the comparison which allows for direct comparison of temperature effects.

Efficient homing to the natal spawning area and precise timing of the migration are critical to optimize energy use. In addition, Pacific salmonids are anticipated to choose low-speed or reverse-flow current paths (Hinch & Rand, 1998) and swim at a metabolically optimal speed (Bernatchez & Dodson, 1987; Hinch & Rand, 2000). Swim speed and energy use have been estimated using various tagging technologies, including radio and acoustic biotelemetry, electromyogram telemetry and acoustic accelerometry. Adults in the open ocean, returning adults migrating down the coast and outmigrating smolts have been repeatedly shown to migrate on average at around $1 L_B \text{ s}^{-1}$ (Drenner *et al.*, 2012), which is the metabolically optimal speed as determined in laboratory studies. In the ocean, Pacific salmonids tend to swim consistently and within their aerobic range. Indeed, in one study with *O. nerka*, only 5% of telemetry detections exceeded $2.5 L_B \text{ s}^{-1}$ (Wilson *et al.*, 2014) and only 17% of detections were estimated to be within the range for burst swimming for another study with *O. nerka* (Quinn, 1988). Swim speeds did not differ from ground speeds in the ocean environment, suggesting that *O. nerka* migrate in a directed manner with few deviations and thus minimize wasted energy when returning to spawn (Wilson *et al.*, 2014).

Swim speed increases once returning fishes enter fresh water because they encounter higher flow rates in rivers (Wilson *et al.*, 2014). Indeed, fishes are forced to swim more quickly in river reaches with stronger currents (Hinch & Rand, 1998) and in years when river discharge is unusually high (Hanson *et al.*, 2008). Burst swimming is necessary to successfully negotiate several sections of the Fraser River, BC, including Hell's Gate ($49^\circ 46' 49'' \text{ N}$; $121^\circ 27' 00'' \text{ W}$), a notoriously difficult section located 250 km upstream (Hinch *et al.*, 1996; Hinch & Bratty, 2000), and the spillway below the Seton Dam ($50^\circ 40' 10'' \text{ N}$; $121^\circ 58' 39'' \text{ W}$; Burnett *et al.*, 2014). Pacific salmonids avoid

the high river flows found in the middle of the river and instead exploit the boundary layer adjacent to the substratum to minimize encountered current speeds (Standen *et al.*, 2002). Swimming behaviour varies considerably among individuals and has been related to energy use and successful migration. When high speed currents are encountered, individual *O. gorbuscha* and *O. nerka* either swim quickly through high speed flows or they swim more slowly, presumably seeking out lower speed paths, resulting in increased passage duration (Standen *et al.*, 2002). While burst swimming may be essential to pass a hydrological barrier, hyperactive swimming behaviour and excessive anaerobic metabolism can lead to delayed mortality (Hinch & Bratty, 2000; Burnett *et al.*, 2014). As such, dam engineers and fish managers must take swimming physiology and passage duration into account when designing fish ladders and regulating water flow to minimize anaerobic swimming.

Low energetic condition (Crossin *et al.*, 2004; Rand *et al.*, 2006) and disproportionately high levels of energy use (Rand & Hinch, 1998; Macdonald, 2000) have been linked with high en route mortality, providing evidence that energy reserves and energy depletion are important factors determining successful upriver migration. This is especially apparent for the Early Stuart *O. nerka* that enter the Fraser River in early July and encounter a near maximal river discharge (Fig. 1; Rand *et al.*, 2006). Factors leading to low energy reserves (*e.g.* poor ocean productivity) or excessive energy depletion (*e.g.* high water temperature leading to elevated $\dot{M}O_2$ or high water discharge leading to excessive anaerobic metabolism or inefficient swimming) are important considerations for conservation. Fisheries managers should take ocean productivity, energy states of returning fishes, river temperature and river flow into consideration to ensure adequate escapement.

DIGESTION

Pacific salmonids must obtain, digest and assimilate nutrients in order to meet their energetic requirements for growth, health, reproduction and body maintenance. The oxygen cost of searching and obtaining prey has not been well characterized for wild fishes but would vary widely depending on the life stage, prey source and abundance, competition and environment. One study attempted to determine the metabolic cost of wild juvenile *O. kisutch* defending their feeding territories in streams shortly after emerging from the gravel, using tail-beat frequency calibrated with $\dot{M}O_2$ from laboratory studies (Puckett & Dill, 1984, 1985). Territorial fish had a net energy intake advantage over floater fish that do not defend a territory or maintain a station because they had reduced oxygen costs associated with searching for prey, obtaining prey and agonistic activity (Puckett & Dill, 1985).

The metabolic cost of processing a meal is termed the specific dynamic action (SDA) or heat increment of feeding and is typically measured using a respirometer as the increase in $\dot{M}O_2$ above SMR following a meal (Chabot *et al.*, 2016). Most studies with *Oncorhynchus* spp. have been conducted on hatchery-reared *O. mykiss* fed a single meal of pellets to examine how SDA is influenced by variations in diet composition (Medland & Beamish, 1985; LeGrow & Beamish, 1986; Kaczanowski & Beamish, 1996; Eliason *et al.*, 2007, 2008; Seth *et al.*, 2009), swimming (Alsop & Wood, 1997) and hypoxia (Eliason & Farrell, 2014). In general, SDA represented 4–29% of the energy consumed, postprandial $\dot{M}O_2$ peaked at 1.5–2.5 times SMR (estimated to be

between 25 and 80% of AMR) and duration ranged from *c.* 24 to 48 h, depending largely upon the water temperature, size and composition of the meal (Secor, 2009).

It is difficult to extrapolate from these limited studies on hatchery fishes to wild conditions. First, hatchery-reared fishes are under different selection pressures and differ physiologically from their wild counterparts. Secondly, specially formulated pellet diets are optimized for maximal growth and minimal waste and lack much of the non-digestible components (*e.g.* chitin) found in a diet composed entirely of wild prey. In addition, while most studies examine postprandial $\dot{M}O_2$ after a single meal or a daily meal fed at the same time over a series of days [*e.g.* fingerling *O. nerka* fed daily at 0830 hours over 22 days (Brett & Zala, 1975)], wild fishes feed episodically depending on the season, temperature, prey abundance and life stage. For example, fry overwintering in a frozen lake or stream have an extremely low SMR due to the low temperature, a concomitant reduced energetic requirement and reduced prey intake. When the ice melts and temperatures rise, so does prey availability, food intake and $\dot{M}O_2$.

In the wild, fishes must partition oxygen delivery among competing organ systems (*e.g.* swimming muscles, stomach and intestines, and gonads) to complete different tasks simultaneously (*e.g.* swim, digest and sexually mature) because the capacity of the heart is insufficient to perfuse all vascular beds maximally at the same time. The trade-off between swimming and digestion has been examined for both *O. tshawytscha* and *O. mykiss* (Alsop & Wood, 1997; Thorarensen & Farrell, 2006). In both species, fed fish displayed a significantly elevated $\dot{M}O_2$ at each swimming speed but no significant difference in AMR compared with fasted fish. As a result, the U_{crit} was 9–15% lower in fed compared with fasted fish, indicating that SDA represented an irreducible metabolic load and fed fish supported the oxygen demands of digestion at the expense of maximum swimming performance (Alsop & Wood, 1997; Thorarensen & Farrell, 2006). These results are consistent with the idea that AMR in salmonids is limited by oxygen delivery rather than capacity of tissues to consume oxygen.

REPRODUCTION

Successful spawning requires that fishes reach the spawning grounds with sufficient energy to perform a complex suite of spawning behaviours such as holding, digging, charging, posturing, quivering, chasing, biting and spawning itself. The overall energetic cost of migration and spawning has been estimated by comparing gross somatic energy from fish sampled along the migration route (Table II; Idler & Clemens, 1959; Gilhousen, 1980; Williams *et al.*, 1986; Hendry & Berg, 1999; Crossin *et al.*, 2003, 2004). Spawning behaviours represent a sizeable portion of the total energy expenditure from river entry to death: 15–56% for Fraser River *O. nerka*, 35–51% for Bristol Bay *O. nerka* and 47–66% for Fraser River *O. gorbuscha*. Accordingly, energy allocation during migration and spawning can have profound implications for reproductive success. For example, excess energy use during migration will limit the amount of energy available for spawning behaviours and could contribute to pre-spawn mortality. This could be especially problematic for female fishes as they must invest more energy into gonadal development compared with males, although the energetic cost of upriver swimming is similar (gonadal-somatic indices are 11–20% for females but only 1–4% for males; Gilhousen, 1980; Hendry & Berg, 1999). Other more subtle energetic trade-offs may exist on the spawning ground. For example, a male may

TABLE II. Gross somatic energy and overall energy expenditure for *Oncorhynchus nerka* and *Oncorhynchus gorbuscha* during migration and spawning. Distance from river entry to spawning ground is indicated

	Distance (km)	Year	Sex	Gross somatic energy (MJ kg ⁻¹)			Energy expenditure (MJ kg ⁻¹)	
				River entry	Spawning ground arrival	Post-spawn	Energy used during migration	Energy used during spawning
<i>O. nerka</i>								
Fraser River								
Early Stuart	1071	1956 ^a	M	–	–	–	3.5	2.3
			F	–	–	–	5.0	1.9
		1957 ^a	M	–	–	–	3.4	–
			F	–	–	–	4.4	–
		1958 ^a	M	–	–	–	3.7	2.3
			F	–	–	–	4.9	1.9
		1999 ^b	M	9.3	4.2	–	5.1	–
			F	9.0	4.5	–	4.5	–
Chilko	642	1956 ^a	M	–	–	–	2.8	1.9
			F	–	–	–	4.7	2.4
		1959 ^a	M	–	–	–	4.2	1.9
			F	–	–	–	4.1	2.4
		1999 ^b	M	9.9	6.4	4.5	3.5	1.9
			F	9.8	6.3	4.4	3.5	1.9
Horsefly	807	1999 ^b	M	9.1	4.6	3.7	4.5	1.0
			F	9.6	5.0	3.9	4.6	1.1
Adams	480	1958 ^a	M	–	–	–	1.6	2.0
			F	–	–	–	2.3	1.5
		1999 ^b	M	7.9	4.9	3.9	3.1	1.0
			F	8.6	5.3	4.1	3.2	1.2
Weaver	117	1999 ^b	M	7.1	4.7	4.2	2.4	0.4
			F	7.0	4.8	4.0	2.1	0.8
Bristol Bay								
Pick Creek	98	1996 ^c	M	6.4	4.2	3.0	2.2	1.2
			F	6.8	4.9	2.9	1.9	2.0
<i>O. gorbuscha</i>								
Weaver	117	1999 ^d	M	5.4	4.8	4.0	0.6	0.8
			F	6.4	5.3	4.0	1.0	1.3
Seton	323	1999 ^d	M	5.4	4.8	3.5	0.7	1.3
			F	6.4	5.0	3.6	1.4	1.4
Ashcroft	330	1983 ^e	M	–	–	–	1.1	1.0
			F	–	–	–	0.9	1.1

M, male; F, female.

^aGilhausen (1980), ^bCrossin *et al.* (2004), ^cHendry & Berg (1999), ^dCrossin *et al.* (2003), ^eWilliams *et al.* (1986).

allocate more energy to compete for access to a female at the expense of longevity on the spawning ground (Healey *et al.*, 2003).

Electromyograph radiotelemetry, heart rate biollogging and direct behavioural observations have enabled researchers to estimate the energetic cost of reproductive behaviours on the spawning ground (Healey *et al.*, 2003; McVeigh *et al.*, 2007; Clark *et al.*, 2009). Holding (maintaining position with minimal swimming) was by far the most frequent behaviour and thus comprised the majority of the daily energy budget for both *O. nerka* and *O. keta* (Healey *et al.*, 2003; McVeigh *et al.*, 2007). After holding, the next greatest energy allocation was towards digging for females and posture displays for males (Healey *et al.*, 2003; McVeigh *et al.*, 2007). Although some activities were energetically costly on a per act basis (*e.g.* chasing), they occurred infrequently and thus did not have a major overall contribution to the overall energy budget (Healey *et al.*, 2003; McVeigh *et al.*, 2007). Subordinate males had a lower daily energy expenditure compared with dominant males (Healey *et al.*, 2003; McVeigh *et al.*, 2007), resulting in an energetic trade-off between strategies.

Aerobic swim performance decreases with increasing sexual maturation in *O. gorbuscha* (Williams & Brett, 1987), *O. tshawytscha* and *O. nerka* (E. Eliason, pers. obs.). For example, U_{crit} of *O. gorbuscha* decreased progressively over the course of the migration: from migrating (males, females: 3.4, 2.8 $L_B s^{-1}$) to spawning (2.3, 2.3 $L_B s^{-1}$) to post-spawn (2.1, 1.7 $L_B s^{-1}$) (Williams & Brett, 1987). How RMR and AMR change with sexual maturation is unknown, although the decrease in U_{crit} of *O. gorbuscha* suggests that AMR may decrease and RMR may increase as gonadal-somatic index increases. Similarly, it is unknown how swim performance and $\dot{M}O_2$ are affected by the progressive decrease in somatic energy and the switch from depleted lipid reserves to increased protein utilization as migration progresses. How oxygen delivery is partitioned between the competing demands of gonadal development and swimming, how exactly energy partitioning differs between males and females given that females must invest more energy into gonad development compared with males (Crossin *et al.*, 2004) and whether individual differences in energy partitioning can be linked with en route or pre-spawn mortality are other unknowns.

TEMPERATURE

Temperature critically affects $\dot{M}O_2$ and has therefore received much research attention over the last 70 years. The general exponential relationship between SMR and an acute increase in temperature (Fig. 2) has been repeatedly described in salmonids (Fry, 1947; Brett, 1971a; Lee *et al.*, 2003b; Clark *et al.*, 2008, 2011; Steinhausen *et al.*, 2008; Farrell, 2009; Eliason *et al.*, 2011, 2013b, c). AMR also increases with increasing temperature up to a point, after which it may plateau or even decline at extremely warm temperatures (Fig. 2). Accordingly, aerobic scope increases with increasing temperature until it reaches a maximal value (at the optimal temperature or T_{opt} for aerobic scope), before declining at high temperatures. At critical temperatures for aerobic scope (T_{crit}), aerobic scope is zero and survival is dependent upon anaerobic metabolism and consequently short term (Pörtner & Knust, 2007).

The temperature and $\dot{M}O_2$ relationship, coined a Fry curve for aerobic scope (Farrell, 2009), has fundamental ecological implications for all fishes. In recent years, this has been particularly evident for adult Pacific salmonids performing their upriver spawning migration when an individual fish can encounter a broad range of temperatures (*e.g.*

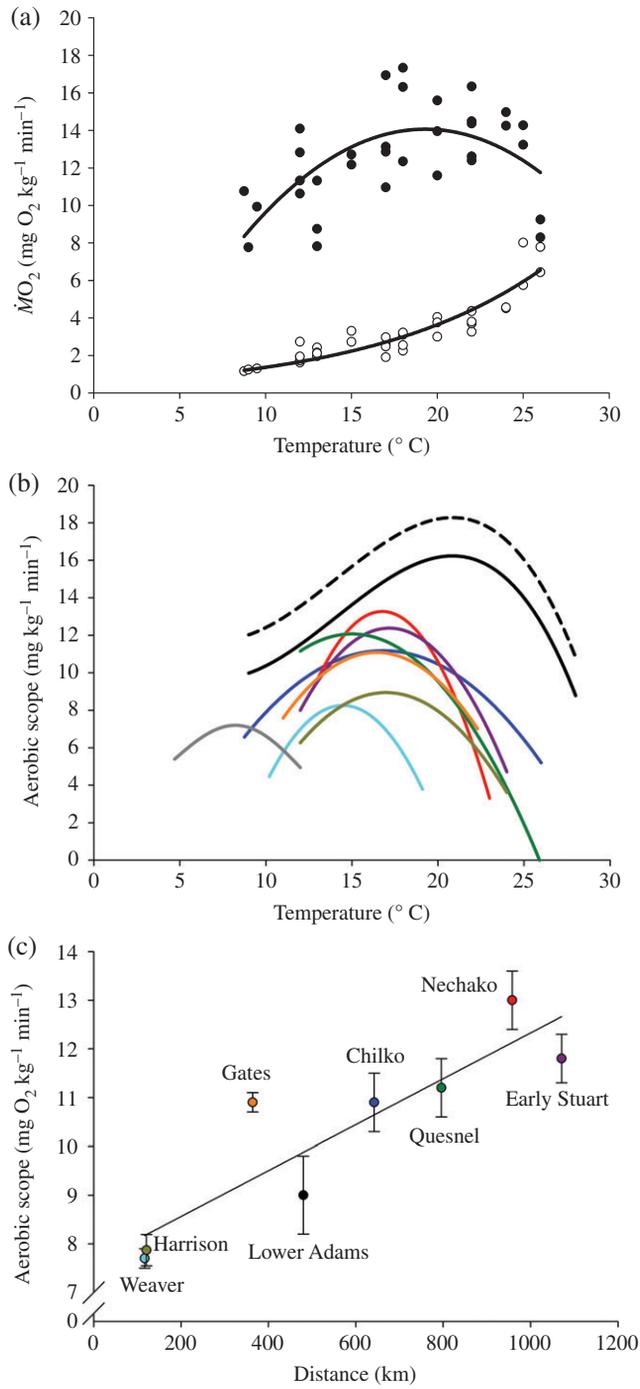


FIG. 2. Legend on next page.

8–22° C in the Fraser River) over a short migration window (e.g. 4 weeks) (Fig. 3; Patterson *et al.*, 2007; Drenner *et al.*, 2014). Climate change-induced increases in river and stream temperatures have created lethal conditions for many populations (Farrell *et al.*, 2008; Mathes *et al.*, 2010), raising conservation concerns. Warm temperatures have numerous adverse effects which may contribute to increasing en route mortality, including enhanced disease development, increased rates of energy expenditure and additional stress (Hinch & Martins, 2011). Recently, at least some of the en route mortality has been attributed to insufficient aerobic scope to meet the energetic demands to migrate upstream (Farrell *et al.*, 2008, 2009; Eliason *et al.*, 2011, 2013b). Indeed, the maximum summer river temperature recently experienced in the Fraser River catchment (c. 22° C) exceeds the optimal thermal window (set at 90% of aerobic scope at T_{opt}) for every population of *O. nerka* examined to date [*i.e.* Early Stuart, Chilko, Quesnel, Nechako, Gates, Weaver and Harrison (Eliason *et al.*, 2011, 2013c)]. Biotelemetry studies have confirmed that Fraser River *O. nerka* fail to reach spawning grounds when fish experience temperatures approaching their population-specific T_{crit} for aerobic scope (c. 20° C for Weaver *O. nerka*; Farrell *et al.*, 2008; Mathes *et al.*, 2010). Similarly, high mortality occurred when river temperatures approached upper critical thresholds (21–24° C) for endangered Snake River *O. nerka* (Keefer *et al.*, 2008a).

In view of the pervasive negative effects of supra-optimal temperature, Pacific salmonids are known to avoid high river temperatures [*e.g.* >19° C for *O. nerka* (Hodgson & Quinn, 2002)] by timing their migration to occur before or after peak river temperatures. Alterations in migration timing are limited, however, by the highly conserved spawning date and the fishes' limited energy stores. Many populations take advantage of a thermally heterogeneous migration environment to seek out cold-water refugia to avoid high temperature (Berman & Quinn, 1991; Goniea *et al.*, 2006; Keefer *et al.*, 2008b; Mathes *et al.*, 2010), whereas other populations have limited thermal refugia available during much of their migration (Donaldson *et al.*, 2009). Individuals that sought cool water refugia when river temperature was elevated had enhanced survival compared with fish that remained in the warm river (Mathes *et al.*, 2010). According

FIG. 2. (a) Changes in active metabolic rate (AMR, ●) and routine metabolic rate (RMR, ○) as a function of temperature for Chilko *Oncorhynchus nerka*. Each point corresponds to an individual fish, an exponential equation was fitted to the RMR data ($y = 0.5137e^{0.0979x}$), a polynomial quadratic equation was fitted to the AMR data ($y = -5.0733 + 1.9833x - 0.0514x^2$). Data are from Eliason *et al.* (2011). (b) Aerobic scope (the difference between active metabolic rate and resting metabolic rate) for *Oncorhynchus* spp. from the Fraser River: eight populations of *O. nerka* [Chilko (—), Nechako (—), Early Stuart (—), Quesnel (—), Gates (—), Weaver (—), Harrison (—)], male (---) and female (—) *Oncorhynchus gorbuscha* and Chehalis (—) *Oncorhynchus kisutch*. Chehalis *O. kisutch* spawn in the winter and have a correspondingly lower thermal tolerance compared with Pacific salmonids that migrate upstream during peak summer river temperatures (e.g. Chilko, Quesnel, Nechako and Gates *O. nerka*). *Oncorhynchus gorbuscha* have superior thermal tolerance and aerobic scope compared with other Fraser River Pacific salmonids and thus may be better able to cope with climate change. *Oncorhynchus nerka* data are from Lee *et al.* (2003b); Eliason *et al.* (2011, 2013c), *O. gorbuscha* data are from Clark *et al.* (2011) and Chehalis *O. kisutch* data are from Lee *et al.* (2003b). (c) Aerobic scope as a function of migration distance for eight populations of *O. nerka* ($y = 7.619 + 0.0047x$; $r^2 = 0.80$, $P < 0.01$). Weaver and Harrison are coastal populations with short, easy migrations (c. 120 km) and they have a correspondingly lower maximum aerobic scope compared with upriver *O. nerka* populations with long, difficult migrations (e.g. Chilko, Nechako, Early Stuart and Quesnel swim through Hell's Gate and travel 642–1071 km). Data are from Lee *et al.* (2003b), Eliason *et al.* (2011, 2013c).

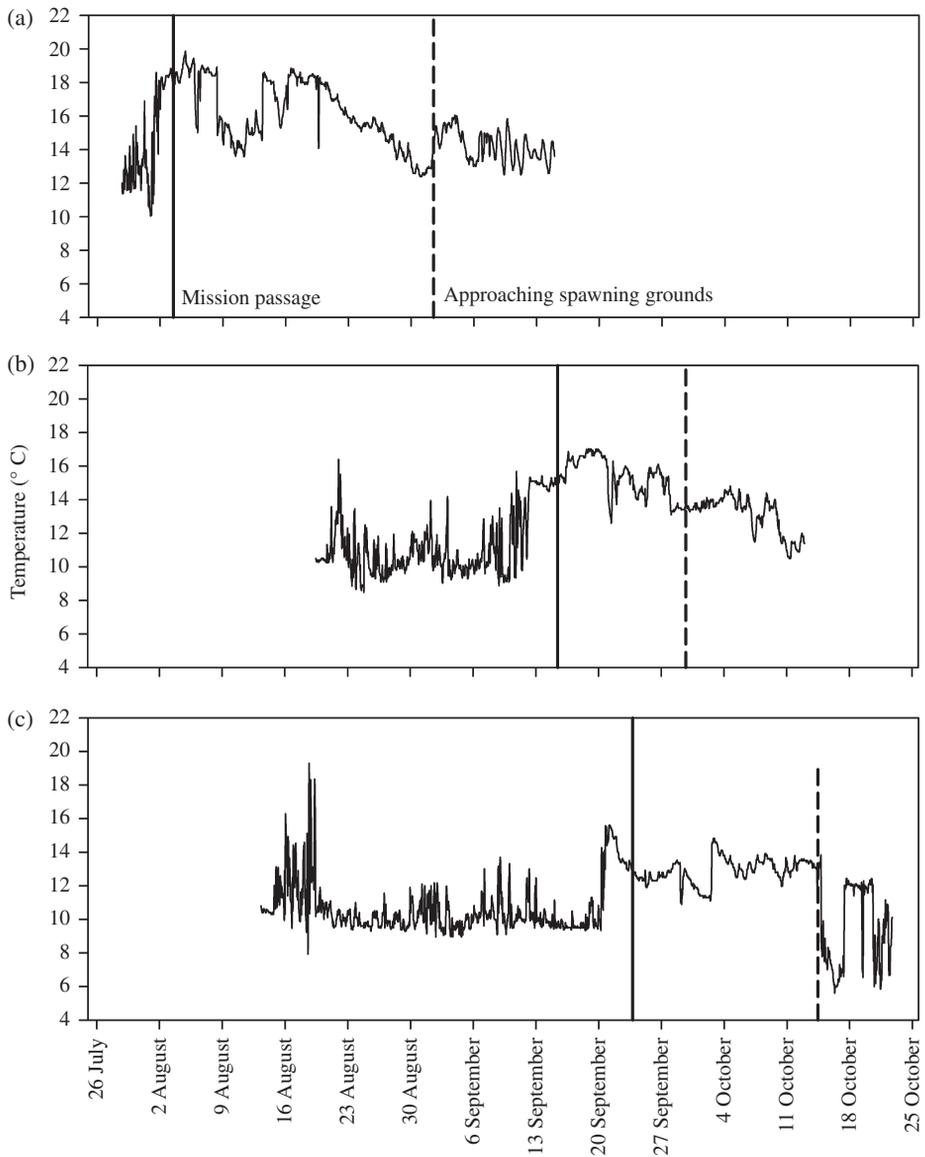


FIG. 3. Hourly temperature recordings from iButton thermal data loggers (www.ibuttonlink.com) recorded from individual *Oncorhynchus nerka* from three populations (a) Late Stuart (summer run; migration distance = 970 km), (b) Weaver (late run; migration distance = 117 km) and (c) Late Shuswap (late run; migration distance = 480 km) from the time of release in the ocean (Johnstone Strait or Juan De Fuca Strait) until they reached their spawning ground. —, when the fish passed Mission (hydroacoustic facility located c. 70 km upstream, passage typically occurs 2–3 days after the fish enter fresh water); - - -, when the fish were approaching the spawning ground. See Fig. 1. Data were kindly provided by LGL Limited (www.lgl.com).

to bioenergetics modelling, Copper Creek *O. nerka* in Haida Gwaii must seek out temperatures $<10^{\circ}\text{C}$ to have sufficient energy to spawn (Katinic *et al.*, 2015) because they return to fresh water for an unusually long residency time before spawning (120 days).

Complex trade-offs between competing physiological requirements complicate behavioural thermoregulation. For example, adult Lake Washington *O. nerka* spend several months prior to spawning at moderate temperatures (*c.* $9\text{--}11^{\circ}\text{C}$) over the warmer (and colder) available temperatures, probably because they balance reproductive maturation with energy conservation (Newell & Quinn, 2005). Conversely, the yet unexplained early entry of late-run *O. nerka* into the Fraser River has exposed them to a much higher river temperature, which has been associated with unusually high river mortality rates (Hinch *et al.*, 2008, 2012). More generally, migrating fishes not only need to balance between choosing cold temperatures to minimize SMR (to conserve energy stores) and pathogen growth (to reduce disease susceptibility) but also must retain sufficient aerobic scope for the swim task ahead, and this temperature may be very near the T_{opt} for aerobic scope (Lee *et al.*, 2003*b*; Eliason *et al.*, 2011). Similarly, rates of reproductive maturation and recovery from exhaustive exercise (*e.g.* after ascending a fish ladder like that at Seton Dam) may be favoured at temperatures corresponding to T_{opt} for aerobic scope, although this idea remains to be tested experimentally. Conversely, searching for navigational cues, avoiding predators (marine, aerial and terrestrial) and adverse environmental conditions (low dissolved O_2 levels, toxicants and salinity) may cause a fish to prefer or unexpectedly encounter sub-optimal temperatures for aerobic scope.

As such, there is no single ideal temperature for all fishes and selection pressures will vary depending on the time, location, environmental conditions (*e.g.* light and dissolved oxygen levels), predator and prey abundance and behaviour and physiological state of the fish. For example, juvenile *O. nerka* commonly perform a diel vertical migration in their nursery lake (Levy, 1990; Brett, 1995). This daily migration behaviour has been postulated to be a three-way compromise between foraging in prey-abundant water, predator avoidance by using crepuscular feeding and the optimization of metabolic efficiency by digesting at a colder temperature because of the lower associated SMR (Levy, 1990; Scheuerell & Schindler, 2003). As another example, *O. kisutch* fry in Bear Creek, Alaska, exploit the thermal heterogeneity in their environment to forage on *O. nerka* eggs in cold habitats ($6\text{--}7^{\circ}\text{C}$) at night and then migrate 350–1300 m to warmer water ($9\text{--}11^{\circ}\text{C}$) in order to increase their metabolic rate and maximize assimilation efficiency (Armstrong *et al.*, 2013). Thus, food availability, predators and feeding strategies may greatly influence thermal preference behaviours in Pacific salmonid species in different ways and these preferences may be independent of their respective T_{opt} for aerobic scope. Therefore, while T_{opt} for aerobic scope sets the maximum capacity for activity, many competing factors are likely to influence the thermal environment that is actually used.

LOCAL ADAPTATION

Oncorhynchus spp. are well known to return to their natal streams to spawn. Some species return with strong fidelity to their home streams (*e.g.* *O. nerka*) while others exhibit weaker homing (*e.g.* *O. gorbuscha*). Natal homing has resulted in reproductively isolated populations within a given catchment (Beacham *et al.*, 2005). Species

and populations encounter widely varying environmental conditions (*e.g.* temperature, dissolved oxygen, salinity, light, currents, substrata, prey species, predators and fishing pressure) throughout the geographical range. As such, *Oncorhynchus* spp. are postulated to be locally adapted to their specific environmental conditions (Taylor, 1991; Fraser *et al.*, 2011).

Since *Oncorhynchus* spp. have a single opportunity to spawn, the upriver adult spawning migration is predicted to be under especially strong selection pressure. Upriver migration conditions vary considerably, even across populations within a single catchment, depending on when the fishes enter the river and where they spawn. For example, Fraser River *O. nerka* populations encounter variable migration distance (*c.* 100–1200 km), elevation (*c.* 10–1200 m), river discharge (*c.* 2000–10 000 m³ s⁻¹) and temperature (*c.* 8–22°C). As such, some populations are faced with a considerably more difficult upriver migration (long distance, high elevation, strong river flow and hydrologically challenging barriers) than others. Indeed, maximum aerobic scope was strongly correlated with upriver migration difficulty in Fraser River *O. nerka* populations (Fig. 2; Eliason *et al.*, 2011, 2013c). Specifically, interior populations with long and arduous migrations (*e.g.* Early Stuart travel >1000 km to reach their spawning grounds; maximum aerobic scope = 369 µmol kg⁻¹ min⁻¹) had significantly higher maximum aerobic scope compared with coastal populations with short, easy migrations (*e.g.* Harrison and Weaver Creek *O. nerka* travel *c.* 120 km to reach their spawning grounds; maximum aerobic scope = 241–247 µmol kg⁻¹ min⁻¹).

Populations also appear to be locally adapted to their specific thermal conditions. Populations of adult Fraser River *O. nerka* and *O. kisutch* maintained maximum aerobic scope across the range of temperatures that they typically encounter (Lee *et al.*, 2003b; Eliason *et al.*, 2011, 2013c). In contrast, Fraser River *O. gorbuscha* have an exceptionally high thermal tolerance (Fig. 2; Clark *et al.*, 2011). T_{opt} for aerobic scope (21°C) corresponded with historic maximum rather than modal river temperatures and maximum aerobic scope was maintained across a broad range of temperatures [*c.* 14–26°C (Clark *et al.*, 2011)]. This suggests that *O. gorbuscha* may possess a physiology to better cope with future climate conditions compared with other Pacific salmonids.

A fundamental concern for hatchery managers is how wild fishes compare with their hatchery-reared counterparts, which are the subjects of most experimental work and are released to stock fish populations. Hatchery-reared fishes experience different selection pressures during rearing compared with wild fishes. For example, hatchery-reared fishes are typically raised en masse in a temperature-controlled, well-oxygenated environment with a surplus of food and no predators. They live in close proximity to conspecifics and thus social cues could play an important role in energy use. In contrast, wild fishes must obtain prey and escape predators, choose a suitable habitat and cope with variable environmental conditions. Wild fishes must prioritize energetic demands among competing organ systems to simultaneously swim, eat, grow, escape or reproduce.

Survival and fitness tend to be higher for wild fishes compared with hatchery-raised fishes (Jonsson & Jonsson, 2006; Araki *et al.*, 2008; Drenner *et al.*, 2012). The resource-rich environment found in hatcheries has generally selected for high growth rates at a cost of reduced swim performance (Bams, 1967; Fleming *et al.*, 2002), possibly due to elevated SMR leading to decreased aerobic scope. Furthermore, wild *O. mykiss* had substantially higher mass-adjusted $MO_{2\text{max}}$ (431–723 mg kg^{-0.87} h⁻¹) when compared with hatchery-reared conspecifics (350–375 mg kg^{-0.87} h⁻¹) (Duthie,

1987; Gamperl *et al.*, 2002). In contrast, another study found no difference in aerobic scope between hatchery and wild *O. mykiss* raised in a common hatchery environment when tested at moderate temperatures (5–20° C), although aerobic scope was significantly higher at 25° C for wild fish (Dickson & Kramer, 1971). The interaction between rearing environment and genetics, and the influence of testing conditions clearly requires further investigation.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Numerous anthropogenic influences are negatively affecting the energetics and cardiorespiratory physiology of Pacific salmonids throughout their North American range. Warming ocean and river temperatures are key challenges. For example, mean summer Fraser River temperatures have increased by *c.* 2° C since the 1950s and are expected to continue along the same trajectory (Morrison *et al.*, 2002; Ferrari *et al.*, 2007). Most Fraser River *O. nerka* populations are already close to the upper limit of their functional thermal tolerance during their upriver migration. Indeed, there is only 2–4° C between T_{opt} for aerobic scope and the estimated upper functional thermal limit for upriver migration. Current maximum Fraser River temperatures (*c.* 22° C) exceed the optimal thermal range for the *O. nerka* populations examined to date (Eliason *et al.*, 2011, 2013c). While populations of Chilko *O. nerka* and *O. gorbuscha* can perform at higher temperatures than other populations and may be better able to cope with further warming, many *O. nerka* populations appear to be in peril. In order to survive rapid changes, populations may need to behaviourally alter their migration timing to avoid high temperatures and physiologically adapt to increase their thermal tolerance (Eliason *et al.*, 2011).

Physiological thermal tolerance in fishes is hypothesized to be determined in the first instance by oxygen and capacity limitations in the organ systems that deliver oxygen from the environment to the tissues (termed the oxygen and capacity-limited thermal tolerance hypothesis; Pörtner, 2001). The collapse in aerobic scope above T_{opt} is triggered by reduced scope for heart rate (Farrell *et al.*, 2009; Eliason *et al.*, 2013b). Accordingly, adaptations that enable the heart to beat normally and increase with temperature are predicted to confer a higher thermal performance. For example, Chilko *O. nerka* have a higher density of adrenaline-binding ventricular β -adrenoceptors, which are known to enhance cardiac capacity during exercise and at temperature extremes (Eliason *et al.*, 2011). This mechanism may help explain why Chilko *O. nerka* have a higher and broader thermal window for performance compared with co-migrating Nechako *O. nerka* (Eliason *et al.*, 2011). Recently, maternally mediated indirect genetic effects were shown to contribute to cardiac performance and thermal tolerance in *O. tshawytscha* (Muñoz *et al.*, 2014). Specifically, maternal effects associated with egg size influenced scope for heart rate. This type of indirect effect could be an additional adaptive mechanism leading to enhanced thermal tolerance. There are other examples where it appears that species of the *Oncorhynchus* genus have adapted physiologically to a higher temperature. For example, stream-dwelling redband trout *O. mykiss*, which are found in Oregon (*Oncorhynchus mykiss newberri*), Idaho (*Oncorhynchus mykiss gairdneri*) and California (*Oncorhynchus mykiss stonei*), experience and survive water temperatures exceeding 29° C (Rodnick *et al.*, 2004) and adaptive heat shock responses have been identified in populations from warm

environments in Idaho (Narum *et al.*, 2013). As another example, *O. mykiss* have been successfully transplanted world-wide, even to the southern hemisphere where no endemic salmonid is found. *Oncorhynchus mykiss* in Western Australia have undergone passive selection over 19 generations to tolerate warmer temperatures compared with other populations, which may be due to enhanced cardiac performance at high temperature (Molony *et al.*, 2004; Chen *et al.*, 2015). In addition, one study with juvenile *O. tshawytscha* indicates that Pacific salmonids do have the physiological and genetic capacities to increase their thermal performance of cardiac function in response to warming temperatures, although the upper thermal limit was constrained to 24.5°C (Muñoz *et al.*, 2015). The heritability of thermal performance of aerobic scope and cardiac function and the rates of adaptation require intensive and immediate research attention in order to predict whether North American salmonid populations will be able to keep pace with current rates of river warming.

Habitat degradation is also a major conservation concern. The importance of habitat heterogeneity is exemplified by *O. kisutch* in Bristol Bay, where juveniles can exploit a thermally heterogeneous environment to maximize both feed intake and digestive efficiency (Armstrong *et al.*, 2013). Hydroelectric dams are common on salmonid-bearing rivers throughout North America, some of which can generate extremely high flows that may impose excessive burst swimming and a lethal anaerobic load on individual migrating fishes (Burnett *et al.*, 2014). Toxicants (*e.g.* dehydroabietic acid, a toxic component of pulp-mill effluent) and diseases (*e.g.* *Parvicapsula minibicornis* and *Saprolegnia* spp.) are known to impair aerobic scope and swim performance in Pacific salmonids (Jain *et al.*, 1998; Tierney & Farrell, 2004; Wagner *et al.*, 2005). It has become abundantly clear that native habitat integrity should be maintained and managers and engineers need to take great care to ensure that the fish passageways align with fish physiology. Specifically, water flow should not induce excessive anaerobic swimming and temperatures should be maintained within the optimal thermal range for aerobic scope whenever possible.

Fisheries management can benefit from incorporating physiological knowledge into models to estimate energy use and mortality in Pacific salmonids. For example, models based on aerobic scope and thermal tolerance were used to predict how often population-specific thresholds will be exceeded in the future (Hague *et al.*, 2011). Models integrating energetic condition and energy use also evaluated how past and future environmental conditions (*e.g.* temperature and discharge) affect migration success (Rand *et al.*, 2006). Bioenergetic models have been developed using $\dot{M}O_2$ to examine growth and energy use in the wild (Trudel *et al.*, 2004; Trudel & Welch, 2005), although the researchers caution against extrapolating across species as bioenergetics models developed for one species were shown to be inappropriate predictors for other species.

FUTURE DIRECTIONS

Despite the considerable amount of research focusing on energetics and $\dot{M}O_2$ in Pacific salmonids, critical knowledge gaps still remain (many of which have already been highlighted). For example, much research has focused on certain species (*e.g.* *O. nerka*), with others have been virtually ignored (*e.g.* *O. keta*), largely due to

the relative commercial importance of the different species. Furthermore, while salmonids in the Fraser River have received a lot of cardiorespiratory research attention, data are severely lacking for fishes from many other important catchments (e.g. Skeena, Bristol Bay, Columbia and Sacramento). In addition, the vast majority of research has focused on the freshwater environment, especially the adult upriver migration, while the physiology of fishes in the marine environment is largely unexplored.

Significant events in the anadromous Pacific salmonid life cycle are the outbound and return migrations between fresh water and seawater. Despite a strong biological and management interest in these key transitions, the energetic costs of the extensive morphological, physiological and behavioural changes associated with salinity transition have received little attention. The studies conducted to date indicate that the metabolic response to changes in salinity depends on the life-history stage. $\dot{M}O_2$ increased with salinity in *O. mykiss* and *O. tshawytscha* fry reared in fresh water and then acclimated to a range of salinities (Rao, 1968; Morgan & Iwama, 1991), possibly indicating an elevated cost of osmoregulation at higher salinities at the fry stage. In contrast, $\dot{M}O_2$ did not differ in *O. kisutch* smolts held for 6 weeks in fresh water, isosmotic salinity and seawater (Morgan & Iwama, 1998). Sexually maturing adult *O. nerka* intercepted in the ocean while en route to the Fraser River had significantly higher routine and active $\dot{M}O_2$ after acclimation for 1 month in seawater compared with 2 months in fresh water (Wagner *et al.*, 2006). As such, metabolic costs may be substantially reduced for sexually maturing adult *O. nerka* once they enter fresh water, although the observed differences may have been due to an elevated stress response in the fish held in seawater as they were long overdue for the transition to fresh water. Clearly, more research is needed to better understand the energetics associated with salinity transition in Pacific salmonids. This critical information will also enable bioenergetics modelling to estimate energy use in fishes migrating in both seawater and fresh water.

Considering that Pacific salmonids are often found in sympatry throughout North America, few studies have specifically compared how species differ in their energetics and $\dot{M}O_2$. For example, juvenile *O. mykiss* and *O. kisutch* co-habit many coastal streams, partitioning the habitat. *Oncorhynchus kisutch* fry hatch earlier and occupy the preferred low speed pools while *O. mykiss* occupy faster speed riffle habitat (Van Leeuwen *et al.*, 2011). A metabolic trade-off appears to exist between species: *O. mykiss* have a higher $\dot{M}O_{2max}$, aerobic scope and swim performance which may confer an enhanced ability to hold in the fast-speed environments compared with *O. kisutch* (Van Leeuwen *et al.*, 2011). *Oncorhynchus mykiss* have a lower growth efficiency compared with *O. kisutch*, but they may encounter more prey in riffles and thus be able to maximize food consumption to compensate for a shorter growing season. As another example, Fraser River *O. gorbuscha* are more energetically efficient upriver migrators compared with co-migrating *O. nerka* (Crossin *et al.*, 2003). In addition, Fraser River *O. gorbuscha* have a superior aerobic scope compared with *O. nerka*, although it is noteworthy that *O. gorbuscha* display much more interindividual variability in $\dot{M}O_2$ and swim performance (Williams *et al.*, 1986; MacNutt *et al.*, 2006; Clark *et al.*, 2011). Similarly, few studies have specifically examined sex-specific differences in $\dot{M}O_2$. In fact, a single study with *O. gorbuscha* reported that females have significantly reduced aerobic scope compared with males (Clark *et al.*, 2011). Given the obvious sexual dimorphism in Pacific salmonids

and the disparity in the energetic investment in gonadal growth (Crossin *et al.*, 2004), sex-specific differences in $\dot{M}O_2$ and energetics deserve considerable research attention.

CONCLUSIONS

For fish biologists to make reliable predictions, there is a need for detailed physiology to understand mechanisms and detailed ecology to understand the habitats and organismal interactions. Details will obviously vary according to species, but by using Pacific salmonids as a case study here, the hope is that the intersections and overlaps between fish physiology and ecology are clearer at least for this genus. A wealth of examples was provided to illustrate the core physiology around oxygen delivery by the cardiorespiratory system and how environmental factors can constrain this delivery system, as originally envisaged by Fry for fishes. A glimpse into the underlying mechanisms was provided, as well as how behaviour must be layered on to this physiological foundation. In the case of Pacific salmonids, physiological knowledge has been already translated into advice for fisheries management. There are many details still missing and these knowledge gaps need to be filled.

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