

RESEARCH ARTICLE

Aerobic scope increases throughout an ecologically relevant temperature range in coho salmon

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ABSTRACT

Aerobic scope (AS) has been proposed as a functional measurement that can be used to make predictions about the thermal niche of aquatic ectotherms and hence potential fitness outcomes under future warming scenarios. Some salmonid species and populations, for example, have been reported to exhibit different thermal profiles for their AS curves such that AS peaks around the modal river temperature encountered during the upriver spawning migration, suggesting species- and population-level adaptations to river temperature regimes. Interestingly, some other salmonid species and populations have been reported to exhibit AS curves that maintain an upwards trajectory throughout the ecologically relevant temperature range rather than peaking at a modal temperature. To shed further light on this apparent dichotomy, we used adult coho salmon (*Oncorhynchus kisutch*) to test the prediction that peak AS coincides with population-specific, historically experienced river temperatures. We assessed AS at 10 and 15°C, which represent a typical river migration temperature and the upper limit of the historically experienced temperature range, respectively. We also examined published data on AS in juvenile coho salmon in relation to new temperature data measured from their freshwater rearing environments. In both cases, AS was either maintained or increased modestly throughout the range of ecologically relevant temperatures. In light of existing evidence and the new data presented here, we suggest that when attempting to understand thermal optima for Pacific salmon and other species across life stages, AS is a useful metric of oxygen transport capacity but other thermally sensitive physiological indices of performance and fitness should be considered in concert.

KEY WORDS: Oxygen- and capacity-limited thermal tolerance, OCLTT, Thermal ecology, *Oncorhynchus kisutch*, Metabolism, Respirometry, Swim tunnel, Exercise, Fish

INTRODUCTION

Thermal performance windows are predicted to have evolved to be as narrow as possible for an animal's life history (Huey and

Kingsolver, 1989; Pörtner and Farrell, 2008). For example, among salmonids, bull trout (*Salvelinus confluentus*) have narrower and colder thermal performance curves than do brown trout (*Salmo trutta*) for metrics such as growth and survival, which correspond with the more alpine habitat of bull trout (e.g. Ojanguren et al., 2001; Selong et al., 2001). To explain the mechanistic basis for thermal performance and tolerance in ectotherms, a leading hypothesis has been termed oxygen- and capacity-limited thermal tolerance (OCLTT) (Pörtner and Knust, 2007). OCLTT proposes that an ectotherm's aerobic scope (AS; the difference between minimum and maximum rates of oxygen consumption, $\dot{M}_{O_2, \min}$ and $\dot{M}_{O_2, \max}$, respectively) is a physiological trait that unifies fitness-related metrics because all activities ultimately require oxygen, and thus can be used to predict thermal performance and perhaps fitness (Pörtner, 2002; Claireaux and Lefrançois, 2007).

The OCLTT hypothesis has been applied to adult sockeye salmon (*Oncorhynchus nerka*) populations undergoing their migration through freshwater to spawning areas, whereby some populations appear to display local adaptation by having AS values that are maximized to accommodate the athletic challenge of their upriver migration and to coincide with the temperatures experienced by previous generations during upriver migration (Lee et al., 2003; Farrell et al., 2008; Eliason et al., 2011). Within this paradigm of local adaptation, it is perhaps not surprising that the ever-increasing peak summer temperatures of the Fraser River, British Columbia, Canada, superimposed on normal annual variability, have caused high en route mortality in sockeye salmon in some years (Patterson et al., 2007; Farrell et al., 2008; Martins et al., 2011; Hinch et al., 2012). Consequently, understanding the underlying cause(s) of migration failure at high temperatures will be fundamental to efforts aimed at conserving the diversity of wild Pacific salmon. Indeed, a progressive decline in AS above historic modal river temperatures has been proposed as one of several potential mechanisms for population-specific en route mortality at high temperatures (Farrell et al., 2008; Hinch et al., 2012). With climatic change occurring at an alarming rate and regarded as a key pressure acting upon Pacific salmon conservation and management (Patterson et al., 2007; Crozier et al., 2008; Bryant, 2009; Martins et al., 2011; Reed et al., 2011), AS has emerged as a potentially useful functional measurement with which to make predictions about the thermal niche of aquatic ectotherms and hence potential fitness outcomes under future warming scenarios.

Nevertheless, some organisms exhibit extremely broad thermal tolerance. For example, depending on acclimation temperature, killifish (*Fundulus heteroclitus*) and goldfish (*Carassius auratus*) can have thermal tolerance ranges in excess of 30°C based on measurements of critical thermal maxima (CT_{\max}) and minima (CT_{\min}), and AS (e.g. Fanguet et al., 2006; Healy and Schulte, 2012; Ferreira et al., 2014). Furthermore, some populations of Fraser River salmon clearly appear to either maintain or even increase AS at

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List of symbols and abbreviations

AS	aerobic scope
CT _{max}	critical thermal maximum
CT _{min}	critical thermal minimum
FAS	factorial aerobic scope
FL	fork length
GCOT _{exer}	gross cost of transport at maximum swimming speed
\dot{M}_{O_2}	rate of oxygen consumption
$\dot{M}_{O_2,max}$	maximum rate of oxygen consumption
$\dot{M}_{O_2,min}$	minimum rate of oxygen consumption
NCOT _{exer}	net cost of transport at maximum swimming speed
OCLTT	oxygen- and capacity-limited thermal tolerance
pO_2	oxygen partial pressure
Q ₁₀	factor by which a given parameter changes with a warming of 10°C
T _{opt,AS}	optimum temperature for aerobic scope
U _{crit}	critical swimming speed
U _{max}	maximum swimming speed

temperatures well beyond the mode for the historically experienced river temperatures during their adult river migration (MacNutt et al., 2006; Clark et al., 2011; Eliason et al., 2013). Indeed, AS in some fish species exhibits a steady increase until near-lethal temperatures are reached (e.g. Fry, 1947; Clark et al., 2013a; Healy and Schulte, 2012; Ferreira et al., 2014; Gräns et al., 2014; Norin et al., 2014), in contrast to those species that appear to have clear peaks in AS as a function of temperature (e.g. Fry, 1948; Fry and Hart, 1948; Lefrançois and Claireaux, 2003; Chen et al., 2015). A broad AS curve implies either that there is a selective advantage to being able to maintain a high AS across the range of temperatures inhabited [i.e. the optimal temperature for AS ($T_{opt,AS}$) spans a broad rather than a narrow range, e.g. Healy and Schulte, 2012; Ferreira et al., 2014; Schulte, 2015; see AS comparisons in Farrell, 2009], or that AS is a performance metric that has limited utility for predicting thermal habitat, performance and fitness.

In light of a rapidly warming world (Root et al., 2003), efforts to clarify the causal mechanism(s) for the effects of temperature on performance in fishes must remain a priority area of research to assist with triage of potential conservation problems and identification of potential mitigation strategies. Therefore, the present study expands on the existing AS datasets for Pacific salmon by examining AS in two populations of coho salmon [*Oncorhynchus kisutch* (Walbaum 1792)] in relation to data on their thermal experiences. Coho salmon have diverse life histories (Sandercock, 1991) but generally spend their first year of life rearing in freshwater streams as fry before migrating to the sea as smolts. They forage and grow in the Pacific Ocean before returning to their natal streams in the autumn and early winter to spawn, generally after ~1.5 years at sea (age 3; Bradford and Irvine, 2000). During their spawning migration, adult coho salmon are thought to conform to the OCLTT hypothesis by achieving peak AS at the water temperatures most commonly encountered during their upstream migration to freshwater spawning areas (Lee et al., 2003; Farrell et al., 2008). We measured AS in adult coho salmon from the Chilliwack River, British Columbia, Canada at 10°C, a temperature commonly encountered both during ocean life (Welch et al., 1995) and during the upstream migration to spawning areas, and after at least 2 days of exposure to 15°C, the extreme upper limit of historically experienced temperatures during their 125 km (~5–7 day) upstream migration to the spawning area. Use of these two key temperatures, coupled with long-term thermal datasets from the relevant watersheds, enabled us to test the prediction that the AS of

adult coho salmon peaks at the temperature(s) most commonly encountered during the upstream migration to spawning areas (here, ~10°C) and declines at a higher temperature (15°C). Furthermore, we assessed whether juvenile coho salmon from the nearby Seymour River, British Columbia, Canada, conform to OCLTT by comparing recent AS data from that life stage (Casselmann et al., 2012) with new temperature records from the freshwater environment that would be predicted to influence the thermal response of AS. For both life stages, we then set our analyses of AS and watershed temperatures within the context of existing knowledge on the thermal ecology of this species, enabling us to assess the potential role of AS in defining thermal niches.

MATERIALS AND METHODS**Animal collection and holding**

Adult coho salmon [total $n=28$; mean±s.e. fork length (FL)=60.6±0.7 cm, range=54–69 cm; mean mass=2.56±0.12 kg, range=1.75–4.29 kg] were collected with a dip-net from a concrete raceway (~8–10°C) at the Chilliwack River Hatchery (A in Fig. 1) on seven occasions between 14 and 29 October 2011. They had completed their migration from the marine environment, a ~125 km upstream swim through the Fraser and Chilliwack Rivers, in less than a week. All fish had been reared and released from the same location ~1.5 years earlier. The fish were transported (~25 min duration) in well-aerated Chilliwack River water (~8–10°C) to nearby Cultus Lake Salmon Research Laboratory (B in Fig. 1), where they were placed in one of two large in-ground concrete ponds (5.3 m diameter, 60 cm water depth) supplied with a continuous flow of water drawn from nearby Cultus Lake (9–10°C). This water temperature mimicked the river temperature experienced while swimming to the spawning area. The temperature in one of the two holding ponds was gradually increased to ~15°C during the first 24 h after fish transfer to simulate an acute temperature experience that was marginally warmer than the maximum temperature revealed in the historic thermal records (see ‘Watershed temperature records’, below, and Results). To warm the water, a second input of water was run through a heater. Each tank was equipped with a submersible pump positioned horizontally along the wall to create a circular water current (~10 cm s⁻¹) and air was pumped through large air stones at all times to maintain water oxygen levels >90% air saturation. Fish were given 2.4±0.4 days (mean±s.e.) at their experimental temperature prior to being used for respirometry measurements (see below). Fish collection, transport and thermal exposure were repeated on seven separate occasions over a period of 24 days to achieve desired sample sizes. Coho salmon (like all Pacific salmon) generally cease feeding prior to river entry (Sandercock, 1991) and so experimental fish were not fed in captivity. All capture, transport, holding and experimental procedures were approved by the Animal Care Committees of the University of British Columbia and Fisheries and Oceans Canada, following guidelines set by the Canadian Council on Animal Care.

Minimum rates of oxygen consumption ($\dot{M}_{O_2,min}$)

The static, intermittent flow-through respirometer devices and methods used to measure $\dot{M}_{O_2,min}$ followed established practices (see Steffensen et al., 1984, 1989; Clark et al., 2013a) and were the same as those detailed in Clark et al. (2011). Briefly, fish were sealed into one of two 138 litre custom-built respirometers that were submerged within a 1700 litre reservoir tank situated adjacent the two holding ponds, and using the same flow-through water supply set at the desired experimental temperature (10 or 15°C). The respirometers were automatically flushed with aerated water for 45 min of every

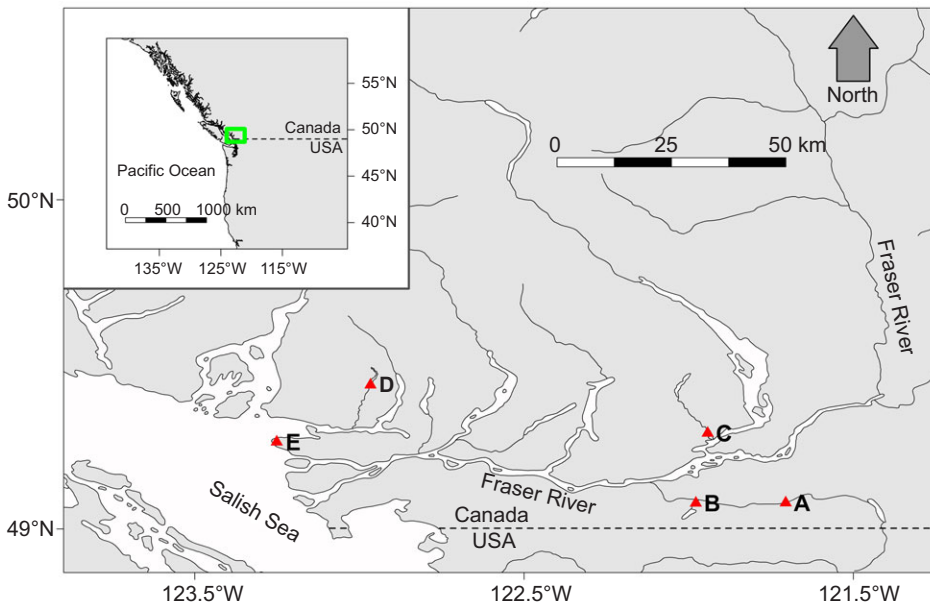


Fig. 1. Map of the study area, with locations relevant to this paper marked by red triangles. A, Chilliwack River Hatchery (where adult salmon were obtained for the present study); B, Cultus Lake Salmon Research Laboratory (where experiments on adult fish took place in the present study); C, Chehalis River Hatchery (where adult fish were obtained in Lee et al., 2003); D, Seymour River Hatchery (where juvenile salmon were obtained by Casselman et al., 2012); and E, University of British Columbia (where experiments took place in Casselman et al., 2012). The relative location of the study area along the west coast of North America is highlighted in green in the inset.

hour, and sealed for \dot{M}_{O_2} measurements during the other 15 min. Oxygen levels within the respirometer water were recorded at all times (at 1 Hz) using oxygen electrodes (Loligo Systems, Tjele, Denmark) situated within a recirculation line that ensured the water was well mixed within each chamber. Each trial continued for 20–26 h (i.e. 20–26 \dot{M}_{O_2} measurements per fish; see Fig. 2) and $\dot{M}_{O_{2,\min}}$ for each fish was calculated as the mean of the lowest three measurements obtained during its trial (Fig. 2). At the end of the measurement period, fish were removed from the respirometers and euthanized by cerebral percussion before being weighed and measured. Seven individuals were tested at each of the two test temperatures (10 and 15°C; total $n=14$). The respirometers were periodically sealed without containing a fish to measure background (microbial) respiration, which was negligible at both temperatures.

Maximum rates of oxygen consumption ($\dot{M}_{O_{2,\max}}$)

Individual fish were netted from the holding tanks for measurements of $\dot{M}_{O_{2,\max}}$ in a 425 litre Brett-type swim-tunnel respirometer (Farrell et al., 2003; Lee et al., 2003) using a protocol similar to that outlined by Clark et al. (2011). Briefly, fish were first given 90+ min to adjust to the tunnel at a water speed of ~ 0.3 FL s^{-1} with aerated, flow-through water at their respective holding temperature (10 or 15°C). The speed of the swim tunnel's impellor was then progressively increased such that the water velocity increased by ~ 0.2 FL s^{-1} each minute until the fish began showing signs of approaching its maximal swimming velocity (U_{\max}), reflected in intermittent burst-and-glide behaviour [a similar protocol enabled rainbow trout to reach speeds 19–59% higher than their critical swimming speed (U_{crit}); Farrell, 2008].

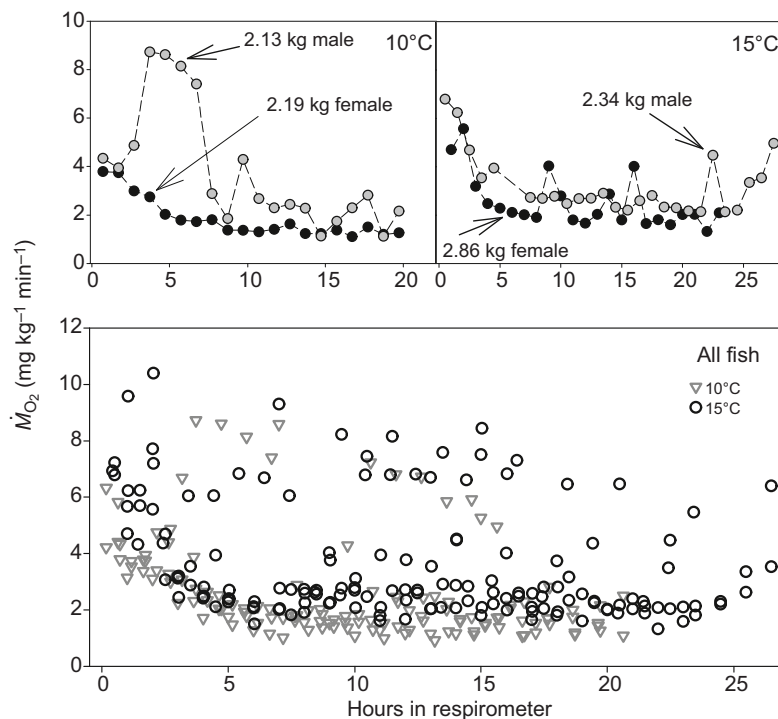


Fig. 2. \dot{M}_{O_2} data used to calculate $\dot{M}_{O_{2,\min}}$ in coho salmon.

Example data from four individuals are shown in the top two panels. The data from all 14 fish ($n=7$ for each temperature) tested in the static respirometers are shown in the bottom panel. For each individual, $\dot{M}_{O_{2,\min}}$ was calculated by taking the mean of the lowest three values of \dot{M}_{O_2} during the measurement period.

The swim tunnel was then sealed for ~20 min so that \dot{M}_{O_2} could be measured. The water speed was usually increased further at the start of the \dot{M}_{O_2} measurement (to ~2.2 FL s⁻¹), but was then modulated as needed to ensure the fish remained maximally challenged without having to rest on the grid at the back of the tunnel, which was occasionally electrified to motivate the fish to exercise. U_{max} was designated as the highest swimming speed that the fish was able to maintain for at least 3 min without having to rest against the rear grid and after correcting for the solid blocking effect of the animal (Jones et al., 1974). $\dot{M}_{O_2,max}$ was calculated from the steepest slope for oxygen partial pressure (pO_2) of water in kPa versus time over any 5 min segment of the ~20 min measurement period. After swim trials, the fish were removed from the tunnel, killed by cerebral percussion, weighed and measured. Experiments were performed on seven individuals at 10 and at 15°C (total $n=14$). Background respiration remained negligible throughout the experimental period.

Data analysis and statistics

Sexes were not obvious based on external morphology in some cases, so the number of males and females in each treatment could only be determined post-experimentation by dissection (for $\dot{M}_{O_2,min}$: 4 females and 3 males at 10°C, 3 females and 4 males at 15°C; for $\dot{M}_{O_2,max}$: 6 females and 1 male at 10°C, 3 females and 4 males at 15°C). Data were combined for males and females for analyses to avoid low statistical power (following Lee et al., 2003). There were no significant differences in fish size (mass in kg or FL in cm) between test temperatures for either the $\dot{M}_{O_2,max}$ or $\dot{M}_{O_2,min}$ measurements (Wilcoxon rank-sum test, all $P>0.2$), or when comparing the mass and length of fish used for measurements of $\dot{M}_{O_2,min}$ versus those used to measure $\dot{M}_{O_2,max}$ (pooled temperatures; $P>0.6$ for both metrics). AS of an individual salmon from the swim tunnel trials was estimated by subtracting the group mean $\dot{M}_{O_2,min}$ at the relevant temperature from that individual's $\dot{M}_{O_2,max}$ (as in Clark et al., 2011). Variability in $\dot{M}_{O_2,min}$ was low at both temperatures (s.d.=0.13 mg kg⁻¹ min⁻¹ at 10°C=10% of grand mean $\dot{M}_{O_2,min}$; s.d.=0.32 mg kg⁻¹ min⁻¹ at 15°C=16% of grand mean $\dot{M}_{O_2,min}$). Gross cost of transport during maximum exercise (GCOT_{exer}; mass-specific oxygen consumption per meter traveled) was calculated as $\dot{M}_{O_2,max}/U_{max}$ (U_{max} converted to m min⁻¹). Net cost of transport at maximum exercise (NCOT_{exer}) was calculated by dividing the AS of an individual by its U_{max} , which removes any variability due to $\dot{M}_{O_2,min}$ and is a true measure for the actual cost of locomotion. The temperature coefficient (Q_{10}) was calculated for \dot{M}_{O_2} , GCOT_{exer} and NCOT_{exer} (not for U_{max} because there was no effect of temperature; see Results) and used to adjust values to exactly 10 and 15°C to account for any temperature deviation, which was always <1°C from the desired temperature.

Wilcoxon rank-sum tests were used for statistical comparisons between 10 and 15°C for $\dot{M}_{O_2,min}$, $\dot{M}_{O_2,max}$, AS, factorial aerobic scope (FAS; i.e. $\dot{M}_{O_2,max}/\dot{M}_{O_2,min}$), U_{max} , GCOT_{exer} and NCOT_{exer}. Values herein are given as means±s.e. Statistical tests were conducted using RStudio (v. 0.98.953, RStudio, Boston, MA, USA; <http://www.rstudio.com/>) with α set at 0.05.

Watershed temperature records

We obtained water temperatures records from a mixture of sources. Data for the Fraser River main-stem were obtained from a long-term database of river temperatures measured from a variety of representative locations [daily means for 1954–1985, 1996–1999 and 2001–2013; Fisheries and Oceans Canada's (DFO) Environmental Watch Program]. The Fraser River is well mixed,

and the internal body temperature of upstream-migrating adult sockeye salmon rarely deviates more than 1°C from the temperatures recorded by the in-river thermal loggers that generated the values in the database we used here (Donaldson et al., 2009). The main-stem of the Fraser River makes up the majority of the migration for many of the populations in the basin (~70% of the migration in the case of Chilliwack River coho salmon). The temperatures experienced in subsequent spawning tributaries can be warmer, cooler or similar to those experienced in the Fraser River, depending on year, location and time of year. Here, we obtained temperature data recorded at the Seymour and Chilliwack River hatcheries (daily means; D and A in Fig. 1, respectively); in the latter case, temperature was measured as the water was drawn from the river (data supplied by DFO's Environmental Watch Program). Thus, even though the thermometers were not placed directly in the Chilliwack River, these temperatures are representative of those experienced by fish both in the river and in the hatchery itself (e.g. rearing juveniles). The Chilliwack River data were used to characterize temperatures experienced during the adult migration period (ca. 1 Oct–30 Nov). The Seymour River hatchery, from which juvenile coho salmon were obtained for measurements of AS (Casselman et al., 2012), draws its water from the reservoir directly upstream (which also supplies the river itself). To supplement the data from the hatchery (daily means from 1 Aug 2007 to 1 Aug 2013), which we expected may have differed somewhat from the in-river temperatures, we installed and maintained two thermal loggers in coho salmon rearing habitat (two locations) in the Seymour River that recorded temperature every 10 min for a 3-year period (8 Aug 2010 to 24 Aug 2013; HOBO Water Temp Pro V2, Onset Computer Corporation, Bourne, MA, USA). Seymour River thermal records were used to characterize the range of temperature experienced by juvenile coho salmon rearing there (May–October) – temperatures that we predicted would shape the thermal response of AS.

RESULTS

Adult coho salmon

\dot{M}_{O_2} progressively decreased after fish were placed in the static respirometers, reaching a stable value within 6–8 h. Thus, 12–20 measurements were used to estimate an individual's $\dot{M}_{O_2,min}$ (Fig. 2). As expected, $\dot{M}_{O_2,min}$ was significantly higher (56%) at 15°C than at 10°C (2.06±0.12 versus 1.32±0.05 mg kg⁻¹ min⁻¹; Wilcoxon rank-sum test, $P<0.001$; Fig. 3) and the Q_{10} was 2.37. U_{max} ranged from 1.90 to 2.41 FL s⁻¹ but was not significantly different between 15 and 10°C (2.13±0.08 and 2.15±0.08 FL s⁻¹, respectively; Wilcoxon rank-sum test, $P=0.65$; Fig. 3). Nevertheless, $\dot{M}_{O_2,max}$ was 19% higher at 15°C than at 10°C (11.71±0.15 versus 9.88±0.54 mg kg⁻¹ min⁻¹; $P=0.018$; Fig. 3) and the Q_{10} was 1.53. As a result, GCOT_{exer} was 20% higher ($Q_{10}=1.20$) at 15°C than at 10°C (0.151±0.005 versus 0.126±0.007 mg O₂ kg⁻¹ m⁻¹; $P=0.011$), but a similar trend in NCOT_{exer} (0.124±0.004 versus 0.109±0.006 mg O₂ kg⁻¹ m⁻¹ at 15 and 10°C, respectively; $Q_{10}=1.29$) did not reach statistical significance ($P=0.053$). Therefore, the increase in GCOT_{exer} was driven by the increased cost of living more so than either a greater swimming effort or a lower mechanical efficiency of locomotion at 15°C. A larger relative increase in $\dot{M}_{O_2,min}$ than in $\dot{M}_{O_2,max}$ between temperatures meant that FAS ($\dot{M}_{O_2,max}/\dot{M}_{O_2,min}$) was 32% higher at 10°C (7.51±0.41) than at 15°C (5.68±0.07; Wilcoxon rank-sum test, $P=0.004$). However, AS was 13% higher at 15°C than at 10°C (9.62±0.14 versus 8.54±0.52 mg kg⁻¹ min⁻¹; Wilcoxon rank-sum test, $P=0.026$;

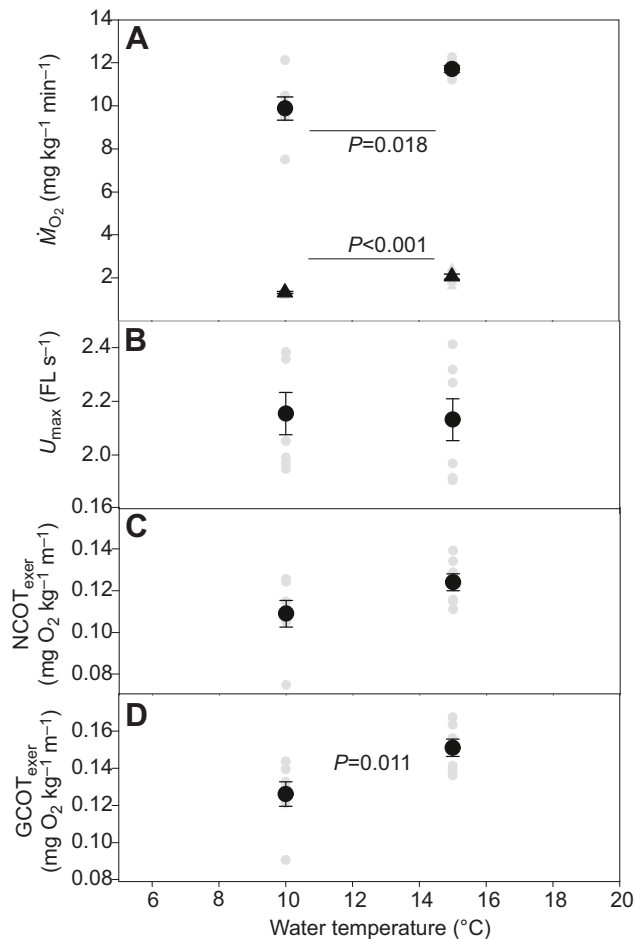


Fig. 3. Metabolic and swimming performance metrics for coho salmon. Mean \pm s.e. (black symbols) for (A) minimum (triangles) and maximum (circles) oxygen consumption rates ($\dot{M}_{O_2, \min}$ and $\dot{M}_{O_2, \max}$, respectively), (B) maximum swimming speed (U_{\max}), (C) net cost of transport during maximum swimming ($NCOT_{\text{exer}}$) and (D) gross cost of transport during maximum swimming ($GCOT_{\text{exer}}$) in adult coho salmon at 10 and 15°C. Values for all individuals are given as light grey symbols. Significant differences are noted by P -values from Wilcoxon rank-sum tests.

Fig. 4A) because of the greater absolute increase in $\dot{M}_{O_2, \max}$ compared with $\dot{M}_{O_2, \min}$ between temperatures.

Fig. 4A places the two AS measurements in the context of historic temperature records for the Fraser and Chilliwack Rivers (white and grey bars, respectively), calculated using daily mean temperatures in the Fraser and Chilliwack systems within 1 month either side of peak migration timing for Chilliwack River coho salmon; i.e. 1 October through 30 November, with a peak migration date of 1 November. These two sites represent 91 and 38 km of the population's 125 km upstream migration to the Chilliwack River Hatchery, illustrating that this population of salmon can maintain high AS over its entire ecologically relevant temperature range for river migration to spawning areas and certainly well beyond the modal temperature for river migration (i.e. ~ 7 – 9°C).

Comparison with juvenile coho salmon

To expand our assessment to the juvenile life stage, we compared published AS data for the Seymour River hatchery population (Casselman et al., 2012; D in Fig. 1) with river temperatures recently recorded in freshwater rearing environments for coho salmon, both

in the Seymour River and from the hatchery where the fish were obtained (light and dark grey bars, respectively, in Fig. 4B). By focusing on water temperatures from 1 May through 31 October, we not only captured the testing dates used by Casselman et al. (2012) but encompassed the period of summer growth (Bisson et al., 1988; Quinn and Peterson, 1996). By doing so, we compared the thermal performance of AS against relevant river temperature records, but did not attempt to assess ontogenic changes in AS because the juveniles and adults assessed in the present study were from genetically distinct populations (Beacham et al., 2011). The Seymour River population (D in Fig. 1) has a shorter migration distance to the ocean (19 km) than does the Chilliwack River population (A in Fig. 1; 125 km), while many other coho salmon populations migrate >400 km to the ocean (Sandercock, 1991). Nevertheless, the Seymour River and Chilliwack River populations share a similar freshwater rearing temperature during the summer growing period (Fig. 4B) and a similar peak smolt outmigration time (i.e. mid-May is when juvenile fish migrate to the ocean).

AS of juvenile Seymour River coho salmon was again maintained over the entire ecologically relevant temperature range that juveniles typically experience during rearing in these watersheds (i.e. ~ 5 – 18°C) and certainly well beyond the modal temperature. However, AS did decline significantly by 33% at 21°C from its numerical peak at 17°C (Casselman et al., 2012), with 21°C being beyond the historic temperatures that Seymour River coho salmon would usually encounter during their juvenile life cycle (Fig. 4B). Importantly, the frequency of encountering temperatures above both 10 and 15°C was greater for juvenile than for adult salmon from these two populations, but neither thermal record shows a modal river temperature at which AS was found to be highest. Instead, AS was either maintained or increased modestly above the modal river temperatures.

DISCUSSION

Pacific salmonids (*Oncorhynchus* spp.) are icons of the Pacific Northwest of North America and utilize aquatic environments that are diverse across life stages, populations and species (Quinn, 2005). During their migration from the Pacific Ocean to freshwater spawning grounds, maturing adult salmon sometimes face extreme environmental challenges (Reed et al., 2011). While there is some evidence that Pacific salmon can temporarily delay river entry or otherwise alter their migration behaviour to avoid extreme conditions (Goniaea et al., 2006; Mantua et al., 2015), in most cases salmon make their migration towards their natal freshwater locale on a relatively fixed schedule (Crozier et al., 2008) and represent a classic example of local adaptation (Wright, 1978). As post-glaciation colonizers of Canada, Pacific salmon are adapted for a life that exploits cold-water habitats, both during their freshwater phase and during their marine phase in the northern Pacific Ocean. They also exhibit specialized traits that are diverse among genetically distinct populations and reflect fidelity to natal environments (e.g. Groot and Margolis, 1991; Crossin et al., 2004). The potential importance of AS logically leads to the prediction that coho salmon should exhibit local adaptation whereby their AS reflects population-specific challenges, including a peak AS over a range of temperatures most commonly encountered and a peak AS that is as narrow as possible for its life history (Pörtner and Farrell, 2008). Therefore, the data generated and synthesized in the present study (Fig. 4) represent a relevant entry into the debate about our ability to predict temperature-specific performance and fitness using the OCLTT hypothesis (Franklin et al., 2009; Clark et al., 2013a,b; Farrell, 2013; Pörtner

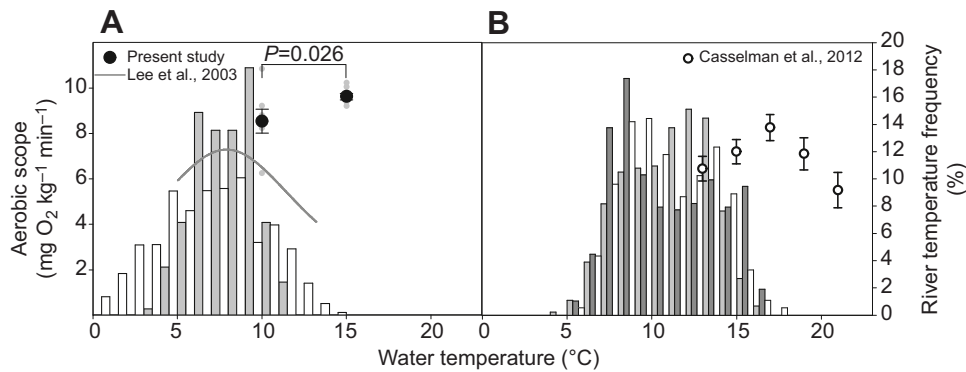


Fig. 4. Aerobic scope data for coho salmon in relation to historic water temperatures. (A) Aerobic scope at two temperatures in adult coho salmon in the present study (black circles; mean \pm s.e. with individual data points in grey) and in a prior study (dark grey line, based on equation given in Lee et al., 2003) on a geographically proximate population of coho salmon with the same peak timing for upriver migration (1 November). The P -value shown for the between-temperature difference is based on a Wilcoxon rank-sum test. The white histogram bars are based on daily mean temperatures for the Fraser River (DFO Environmental Watch Program) for all days from 1 October through 30 November for all available years (1954–1985, 1996–1999 and 2001–2013) in bins of 1°C (e.g. 10.00–10.99°C, 11.00–11.99°C, etc.). The grey bars are binned frequencies of Chilliwack River daily mean temperatures for 1 October through 30 November from all available years (2000, 2006, 2009 and 2011–2013; DFO Environmental Watch Program records). (B) Previously published mean \pm s.e. aerobic scope (open circles) in juvenile (pre-smolt) coho salmon (from fig. 2C in Casselman et al., 2012) obtained from the Seymour River Hatchery in March 2010 at \sim 1 year of age and tested shortly thereafter when they reached 16.9–18.1 g. The only statistically significant pairwise *post hoc* difference in aerobic scope among the five temperatures was between 17 and 21°C (Casselman et al., 2012). Light grey bars represent binned temperature frequencies (as in A) for the period 1 May through 31 October each year from two temperature loggers stationed in juvenile coho salmon rearing habitat in the Seymour River that recorded temperature every 10 min from 8 July 2010 through 24 August 2013. Dark grey bars are similarly binned temperatures for the Seymour River Hatchery, which uses water pumped from Seymour Reservoir (i.e. upstream of a dam on the system), based on daily means from hatchery records from 1 August 2007 through 1 August 2013. White bars are May–October daily mean temperatures for the Chilliwack River for 1999, 2006, 2007, 2009 and 2011–2013. Both the Seymour and Chilliwack River populations hatch in the spring (i.e. April) and rear for \sim 1 year before a peak smolt outmigration time of mid-May.

and Giomi, 2013; Jutfelt et al., 2014; Schulte, 2015), particularly with respect to Pacific salmon about which there is considerable prior knowledge of thermal ecology (e.g. Brett, 1995; Richter and Kolmes, 2005).

Adult coho salmon migration

Our data do not support the prediction that AS in Chilliwack River adult coho salmon peaks at, and declines after, the mode of historically experienced freshwater temperatures during their migration from the ocean to their natal spawning area. Instead, the highest AS measured here (at 15°C) was closer to the historic upper temperature extreme for the past \sim 60 years (Fig. 4A) and the thermal effect on $\dot{M}_{O_2, \min}$ was more than matched by the temperature-related increase in $\dot{M}_{O_2, \max}$. Although the present study is limited to two test temperatures and it was not our objective to define the shape or breadth of the thermal performance curve for AS, this pattern appears to be similar to that reported for Harrison River pink salmon (Clark et al., 2011) and Harrison River sockeye salmon (Eliason et al., 2013), for which AS increased through an ecologically relevant temperature range and peaked at or above the historic extreme high temperature of the river during the spawning migration. These populations have similarly short migration distances. This contrasts with several other populations of sockeye salmon that have been examined to date, with both short and longer migration distances (Eliason et al., 2011), and curiously, the neighbouring Chehalis River coho salmon (Lee et al., 2003), which was reported to have a peak for AS at a temperature close to the mode for river migration (\sim 8°C) and was predicted to have just 66% of peak AS at 13°C (the highest measurement temperature in Lee et al., 2003). We caution that the peak AS for adult Chilliwack River coho salmon was not identified here, and could lie between 10 and 15°C, or even above 15°C and similar to \sim 17°C, which is where peak AS occurs for juvenile Seymour River coho salmon (Fig. 4B) (Casselman et al., 2012). Indeed, it is possible that this population of

coho salmon maintains high AS across a relatively broad thermal range. Nevertheless, our experimental design allowed us to test (1) whether AS is highest at the modal historical river temperature, and (2) whether $T_{\text{opt, AS}}$ integrates and reflects optima for other ecologically relevant performance traits. Oceanic temperatures for coho salmon likely do not exceed \sim 11°C during feeding and coastal migration (Ogura and Ishida, 1992; Welch et al., 1995; Walker et al., 2000), aside from occasional forays of salmon into warmer unmixed coastal surface waters that would not exceed 16°C (Walker et al., 2000). Why this and other salmon populations appear to attain peak AS at or above temperatures that they may only occasionally experience is open to speculation, but it is clear that climatic warming would have to be considerable before this population of coho salmon would have their aerobic capacity challenged.

The marked difference in thermal performance of AS in adult coho salmon between the Chilliwack River (present study; \sim 2.6 kg) and Chehalis River (Lee et al., 2003; \sim 2.4 kg) populations warrants further comment. Peak AS for Chehalis River coho occurred at 8°C and, perhaps simply because of a Q_{10} effect, was slightly lower (7.29 mg O₂ kg⁻¹ min⁻¹; Lee et al., 2003) than reported here for fish at 10°C (8.56 mg O₂ kg⁻¹ min⁻¹). Nevertheless, extrapolating the AS curve for Chehalis River coho beyond the highest measurement temperature (13°C) to 15°C yields an AS (3.05 mg O₂ kg⁻¹ min⁻¹) that is 68% lower than that recorded for adult Chilliwack River coho salmon in the present study (Fig. 4A). Such a large difference could reflect several possibilities, some of which are more likely than others. For example, these are genetically distinct populations (Beacham et al., 2011), which introduces differences in life history and ecology. Yet, the spawning migrations of the Chehalis and Chilliwack River populations (A and C, respectively, in Fig. 1) occur at similar times (early November for peak fish arrival time), with similar migration river distances (115 and 125 km for the Chehalis and Chilliwack Rivers, respectively) and a common migration occurring through the Fraser River main-

stem. Also, the CT_{max} for juveniles is similar for the two populations ($\sim 24^{\circ}C$; McGeer et al., 1991). However, Chehalis River coho salmon were collected and tested later in the year, when temperatures are typically colder ($N=20$ in November and $N=12$ in January; i.e. mostly post-peak arrival time; Lee et al., 2003) compared with the Chilliwack fish in the present study (i.e. latter half of October and tested as late as 5 November; i.e. mostly pre-peak arrival time). Because water temperature tends to decrease throughout the autumn migration period and fish were tested at the river temperature, but only acutely thermally acclimated in both studies, thermal acclimation could have played a role in the differences even though the mean river temperature ($9^{\circ}C$) at the time of experimentation was very similar between the two studies. Inter-year or long-term changes in ocean conditions or foraging success for coho salmon could be a cause of some of the differences between the two studies (the present study took place 10 years after Lee et al., 2003). While the condition factor of the fish was similar between studies (based on a comparison of mass and length measurements), we have no higher-resolution data with which to compare the physical condition or energy stores between the fish tested here and those used by Lee et al. (2003). While there have yet to be any studies examining the role of body condition or relative energy stores on the thermal sensitivity of AS, we would not expect inter-year differences to lead to the major dichotomy in the thermal response of AS between the two studies in question, especially given that these two populations share nearly identical life histories.

Methodological and/or analytical factors could be significant contributors to the discrepancy reported between Chilliwack and Chehalis River coho salmon populations. For example, newer technologies and better practices allow for more continuous and automated measurements of \dot{M}_{O_2} and estimation of $\dot{M}_{O_{2,min}}$ (e.g. Fig. 2). Using a single \dot{M}_{O_2} measurement following an overnight settling period in a swim tunnel to assess $\dot{M}_{O_{2,min}}$ (as in Lee et al., 2003) could be prone to an erroneously high $\dot{M}_{O_{2,min}}$ estimate as \dot{M}_{O_2} is very labile (see Fig. 1) (Brett, 1964). An overestimate of $\dot{M}_{O_{2,min}}$ by 500% as a result of spontaneous activity is a possibility (Fig. 2), which would underestimate AS by more than 300%, and if the Chehalis coho salmon measured at the warmest temperature were more restless, a false peak AS would be generated. The average \dot{M}_{O_2} across a 7-h period (hours 9–15 in Fig. 2) was $3.95 \text{ mg kg}^{-1} \text{ min}^{-1}$ at $15^{\circ}C$ ($1.89 \text{ mg kg}^{-1} \text{ min}^{-1}$ or 92% higher than $\dot{M}_{O_{2,min}}$) and $2.43 \text{ mg kg}^{-1} \text{ min}^{-1}$ at $10^{\circ}C$ ($1.11 \text{ mg kg}^{-1} \text{ min}^{-1}$ or 84% higher than $\dot{M}_{O_{2,min}}$). Thus, while there was a tendency in our dataset for higher variation in \dot{M}_{O_2} , associated with spontaneous activity, at the higher test temperature, the difference is not large enough to explain the discrepancy between the two studies. As a result, we cannot provide a definitive explanation as to why adult coho salmon from these geographically proximate populations appear to diverge in their thermal responses of AS.

The present study found no thermal effect on U_{max} . Meanwhile, the increase in $\dot{M}_{O_{2,min}}$ from 10 to $15^{\circ}C$ ($\sim 0.77 \text{ mg kg}^{-1} \text{ min}^{-1}$) accounted for almost 50% of the increase in $\dot{M}_{O_{2,max}}$ over this temperature range ($\sim 1.83 \text{ mg kg}^{-1} \text{ min}^{-1}$). This may be an important detail in understanding why the historically experienced temperatures for the ~ 5 – 7 day freshwater migration and subsequent weeks until spawning do not align with the thermal characteristics of AS, as would be predicted by OCLTT. To understand this, we must first recognize that fish allocate energy to a variety of activities, and not just river migration, but information on the prioritization and quantitative allocation of oxygen to these activities is poorly understood (Farrell, 2016). A 125 km river migration presumably represents less of an energetic constraint than the migrations carried

out by the populations of sockeye salmon that can migrate up to ~ 1200 km to the interior of British Columbia and have been reported to show a peak AS that coincides with the river migration temperature (Eliason et al., 2011). A migration temperature of $10^{\circ}C$ might reduce $\dot{M}_{O_{2,min}}$ by over 50% when compared with $15^{\circ}C$, and lowers $GCOT_{exer}$ by 20% without compromising U_{max} , energy savings that would prolong life at the spawning area because the fish are fuelled by finite endogenous energy stores. Thus, more energy can be allocated towards reproductive activities, including finishing gonadal development. Indeed, salmonid exposure to temperatures above $13^{\circ}C$, which is ~ 4 – $5^{\circ}C$ above the modal temperature of the river during migration for these populations of coho salmon, just before or during spawning, can compromise gamete quality, lowering fertilization success and embryo survival (Richter and Kolmes, 2005). Also, pathogen growth, which is implicated in pre-spawn mortality of migrating adult Fraser River sockeye salmon (Miller et al., 2014), will occur slower at $10^{\circ}C$ than at $15^{\circ}C$ (Crossin et al., 2008; Bradford et al., 2010; Jeffries et al., 2012a). Indeed, many salmon diseases become virulent at water temperatures above 15.6 – $16.0^{\circ}C$ (Richter and Kolmes, 2005) and fungal infections become especially prevalent at $>18^{\circ}C$ for sockeye salmon (Jeffries et al., 2012a).

Thus, based on the data published to date (including the present study), we propose that peak AS in some populations with particularly challenging migrations may be tied to the modal river temperature during migration, whereas maximal AS in populations faced with short migration distances (perhaps <200 km, like the populations examined here; Clark et al., 2011; Eliason et al., 2013) has an optimal temperature above this mode. Exceptions to this trend do exist. For example, the Chilko Lake sockeye salmon maintain high AS (and survival) well above the temperatures typically experienced, despite having one of the most difficult migrations (>600 km distance, >1100 m elevation; Eliason et al., 2011; Martins et al., 2011). Conversely, Chehalis River coho salmon and Weaver Creek sockeye salmon each face relatively easy migrations (<150 km distance, <150 m elevation), yet appear to have clearly defined peaks in AS that coincide with historical river temperature modes (Lee et al., 2003; Farrell et al., 2008). A further possibility, discussed below, is that early life temperature experiences may influence how AS responds to temperature during adulthood. Although little is known about how AS changes during ontogeny or whether early-life thermal experiences can have carry-over effects for AS into adulthood, we now have rearing temperature data for juvenile coho salmon that can be compared with previously obtained AS data (Casselman et al., 2012).

Juvenile coho salmon

Juvenile coho salmon must establish and defend a territory in streams, actively forage, grow and evade predators before smoltification and migration to the ocean (Sandercock, 1991). These activities all require oxygen in excess of $\dot{M}_{O_{2,min}}$, which is why OCLTT predicts that performance and fitness should be maximized at the same temperature(s) as AS. Here we show that juvenile coho salmon acclimated to $10^{\circ}C$ and with a peak AS at $17^{\circ}C$ (Casselman et al., 2012), $7^{\circ}C$ below their CT_{max} (23.8 – $24.4^{\circ}C$ for six geographically proximate populations from British Columbia including Chilliwack and Chehalis River populations that were acclimated to $6^{\circ}C$; Brett, 1952; McGeer et al., 1991), typically experience environmental temperatures well below the temperature eliciting peak AS. Both acclimation temperature and genetics will be important considerations for future work because CT_{max} was

3–4°C higher (27.6 and 27.9°C) for 11°C-acclimated juvenile coho salmon from two Washington (USA) streams (Konecki et al., 1995a). Yearling coho salmon had a peak cruising speed (i.e. maintained for 1 h) at ~20°C and maintained 85% of this capacity over the temperature range 15 to 23°C (Brett et al., 1958). Similarly, U_{crit} for under-yearling coho salmon peaked at ~17 and ~20°C for acclimation temperatures of 8 and 11°C, respectively, and near-maximal U_{crit} was maintained up to 23°C (Griffiths and Alderdice, 1972). Even so, maximum growth rate for juvenile coho salmon fed to satiation occurs at ~15°C (L. B. Everson, Growth and food consumption of juvenile coho salmon exposed to natural and elevated fluctuating temperatures, MS thesis, Oregon State University, Corvallis, OR, USA; Edsall et al., 1999), whereas optimal rearing conditions and preferred laboratory temperatures may be in the 12–15°C range (Richter and Kolmes, 2005), with the fish behaviourally avoiding temperatures >15°C in such experiments (Brett, 1952; Konecki et al., 1995b; Richter and Kolmes, 2005). Thus, juvenile coho can have a thermal range for peak aerobic capacity that extends well above their preferred temperatures and optimal growth temperatures. Moreover, if coho salmon prefer to perform certain activities at temperatures below that for peak AS, it is not unreasonable to expect in-stream rearing conditions for juvenile coho in the Seymour River to be at a lower temperature as well. Indeed, stream temperatures were never higher than 18°C in these watersheds and typically were between 7 and 15°C during the summer growing period (Fig. 4B). These temperatures would optimize growth, not AS. Of course, the temperatures reported here are not necessarily representative of all the extreme thermal events that can happen across the range of habitats used by coho salmon. For example, experimental logging of the surrounding forests increased the Carnation Creek (British Columbia, Canada) peak summer temperatures from ~10 to ~15°C, and in winter from ~5 to ~7°C, which resulted in earlier coho salmon emergence, a longer growing season and a 47% increase in smolt numbers (Holtby, 1988). Similarly, following a volcanic eruption, summer temperatures in three Washington (USA) streams typically exceeded 20°C (and even reached 29.5°C in some areas), yet coho salmon growth was similar to other watersheds at cooler temperatures considered optimal for growth (Bisson et al., 1988).

Consequently, juvenile and adult coho salmon apparently have an AS that is highest at the upper extreme temperatures that the fish may only occasionally encounter during their life cycle. Thus, ecological considerations must recognize how thermal habitats are behaviourally exploited by an animal, extending the focus beyond the temperature, or range of temperatures, for peak AS, which informs us of the capacity of an animal to supply oxygen to tissues. Rigorous attempts to define thermal niches should extend beyond AS and involve consideration of multiple thermally sensitive indicators of performance and fitness such as disease and fungal resistance, growth performance, survival, osmoregulation and cellular ion homeostasis (e.g. Selong et al., 2001; Martins et al., 2011; Jeffries et al., 2012a,b; Vornanen et al., 2014). Across taxa, we need to understand why limitations to oxygen transport capacity (specifically AS) appear to align with temperature-specific fitness outcomes in some studies (Pörtner and Knust, 2007; Eliason et al., 2011; Martins et al., 2011; Khan et al., 2014; Chen et al., 2015) but not in others (MacNutt et al., 2006; Clark et al., 2011; Overgaard et al., 2012; Ern et al., 2014; Gräns et al., 2014; Norin et al., 2014). Improving our understanding of how AS changes across life stages (e.g. Killen et al., 2007; Clark et al., 2012; Drost et al., 2016) and what proportion of AS needs to be allocated to a specific activity (Farrell, 2016) will ensure an appreciation of why oxygen supply is

not necessarily limiting to fitness-relevant traits (Clark et al., 2013a). In this regard, because of the diverse life histories of Pacific salmon (Groot and Margolis, 1991), these fish will continue to provide useful models for understanding thermal adaptation and how physiological attributes are modulated across life stages, populations and species in a rapidly warming climate.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

G.D.R. and T.D.C. designed and conducted the experiment and analyzed the data, and used some equipment provided by A.P.F. and S.G.H. Further data were collected by M.T.C. G.D.R. wrote the article with input from all co-authors.

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Data availability

The metabolic and swimming data presented here have been publicly archived on Figshare at <https://dx.doi.org/10.6084/m9.figshare.3398356.v1>.

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