RESEARCH ARTICLE

Chum salmon migrating upriver adjust to environmental temperatures through metabolic compensation

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ABSTRACT

Ectotherms adjust their thermal performance to various thermal ranges by altering their metabolic rates. These metabolic adjustments involve plastic and/or genetic traits and pathways depend on species-specific ecological contexts. Chum salmon (*Oncorhynchus keta*) are ecologically unique among the Pacific salmonids as early-run and late-run populations are commonly observed in every part of their range. In the Sanriku coastal area, Japan, early-run adults experience high water temperatures (12–24°C) during their migration, compared with those of the late-run adults (4–15°C), suggesting that the two populations might have different thermal performance. Here, we found population-specific differences in the thermal sensitivities of metabolic rates [resting metabolic rate, RMR, and maximum (aerobic) metabolic rate, MMR] and critical temperature maxima. Using these parameters, we estimated thermal performance curves of absolute aerobic scope (AAS). The populations had different thermal performance curves of AAS, and in both populations high values of AAS were maintained throughout the range of ecologically relevant temperatures. However, the populations did not vary substantially in the peak (AAS at optimal temperature, T_{optAAS}) or breadth (width of sub-optimal temperature range) of the performance curves. The AAS curve of early-run fish was shifted approximately 3°C higher than that of late-run fish. Furthermore, when the data for RMR and MMR were aligned to the thermal differences from T_{optAAS}, it became clear that the populations did not differ in the temperature dependence of their metabolic traits. Our results indicate that chum salmon thermally accommodate through compensatory alterations in metabolic rates. Our results imply that metabolic plasticity and/or the effect of genetic variance on plasticity might play a pivotal role in their thermal accommodation.

KEY WORDS: Metabolic rate, Aerobic scope, Thermal adaptation, Metabolic thermal compensation, Salmonid

INTRODUCTION

Temperature has a profound influence on ectotherm performance through its thermodynamic effects on metabolism. Ectotherms adjust their thermal sensitivities through plastic and/or genetic physiological changes in order to cope with fluctuating environmental temperatures (Angilletta, 2009). Understanding how they do this is a major challenge for researchers. The concept of oxygen- and capacity-limited thermal tolerance (OCLTT) has been widely used to understand the mechanisms underlying responses to temperature in aquatic ectotherms (Pörtner and Farrell, 2008). OCLTT proposes that the absolute aerobic scope [AAS; the difference between resting metabolic rate, RMR, and maximum (aerobic) metabolic rate, MMR] of an ectotherm is a functional metric for thermal performance because most biological processes (e.g. swimming, digestion, maturation) are accomplished through aerobic metabolism. Indeed, AAS has been linked to swimming performance, growth rate and the speed of digestion (Auer et al., 2015; Eliason and Farrell, 2016), and is assumed to be fitness related. Thermal sensitivity of AAS is described by the thermal performance curve (Payne et al., 2016), where AAS increases with temperature up to a peak (which is defined as the optimum temperature of aerobic scope, T_{optAAS}), and declines thereafter. Sub-optimal temperatures are known as pejus temperatures (T_{pej}) and are predicted to have evolved to have as narrow a window as possible (Pörtner and Farrell, 2008; Raby et al., 2016).

Thermal performance curves have been applied to some species of Pacific salmonids. Pacific salmonids generally spend considerable parts of their life at sea, where they experience water temperatures below 10°C (Friedland et al., 2001; Morita et al., 2010; Walker et al., 2000). However, some local populations of Pacific salmonids encounter warmer temperatures during their spawning migration (Eliason and Farrell, 2016). Recent studies have reported local intraspecific adaptation to the thermal regimes and migration difficulties experienced by adult sockeye salmon (*Oncorhynchus nerka*) during their spawning migration (Eliason et al., 2011, 2013; Lee et al., 2003). These studies revealed that sockeye salmon populations adapt their T_{pej} range (between upper and lower T_{pej}) to the ecologically relevant temperature range during their upriver migration, accompanied by changes in T_{optAAS} and the breadth of the T_{pej} range. Such adjustments in sockeye salmon can be attributed to drastic morphological and functional cardiac modifications that have arisen through genetic adaptation (Eliason et al., 2011).

Chum salmon (*Oncorhynchus keta*) have the widest natural geographic distribution of all Pacific salmon species, ranging from Asia to the Arctic coast (Salo, 1991). They are anadromous, but have brief freshwater life-history stages because the fry migrate directly to the sea soon after emergence (Beacham and Murray, 1986; Morita et al., 2015). Different populations that return early or late to their natal stream occur in every part of the chum salmon distribution (Salo, 1991). The Sanriku coastal area of Honshu Island, Japan (Fig. 1A), is one of the southernmost natural spawning regions of the Asian distribution of chum salmon (Kaeriyama, 1989), where early-run and late-run populations return in autumn and winter, respectively (Okazaki, 1982). In this region, sea surface temperature (SST) and river temperature often exceed 20°C at the beginning of the returning season and decrease below 12°C at the end (Fig. 1B) (Tanaka et al., 2000). The lethal temperature for this species has been reported to be 24°C (Schmidt-Nielsen, 1997). Because of the drastically fluctuating SST from autumn to winter,

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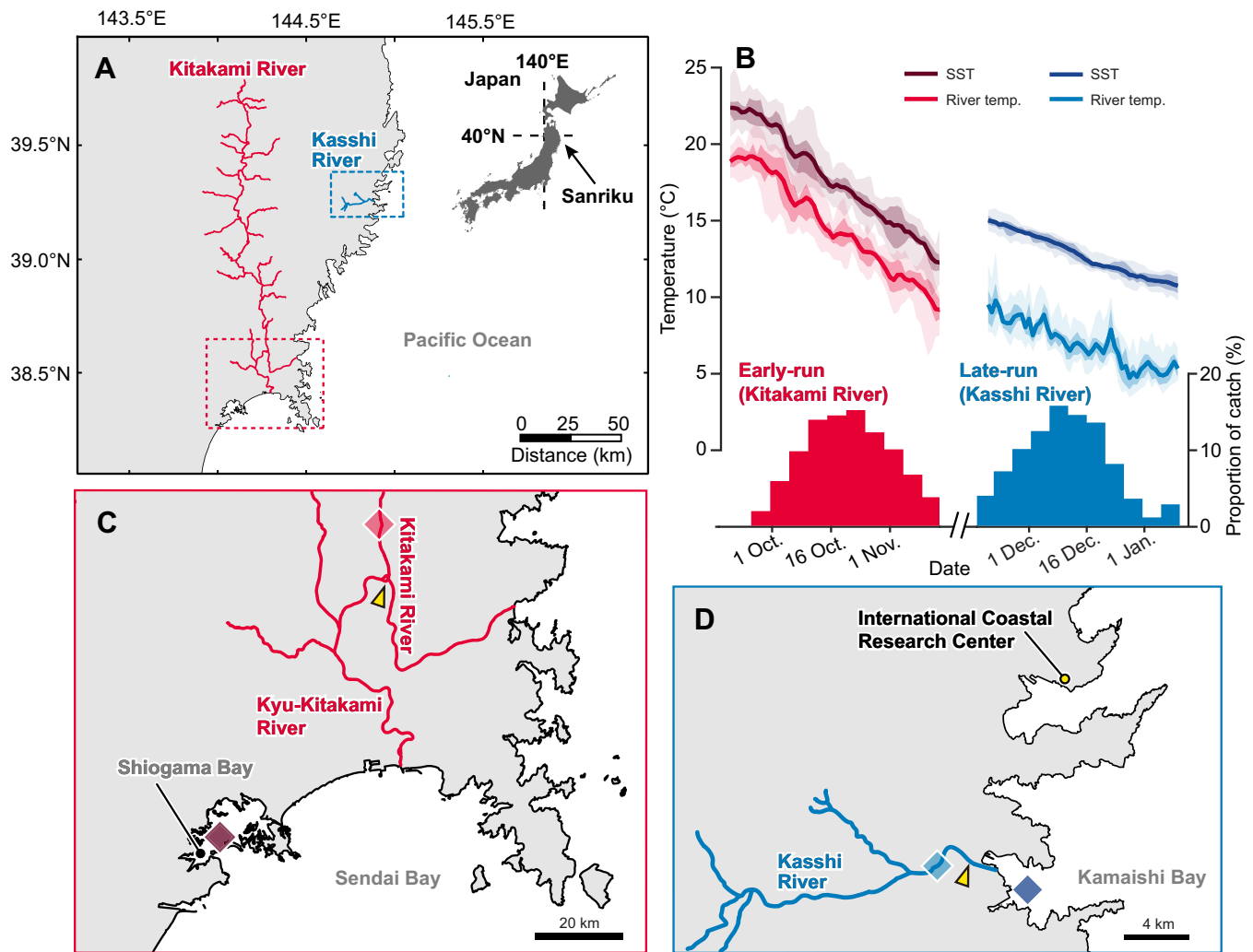*Author for correspondence (t.abe.hpa@gmail.com)

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Fig. 1. Map of the study area and water temperature. (A) The Sanriku coastal area from which fish were obtained for this study. (B) Daily means of river temperature and sea surface temperature (SST) in October (Kitakami River and Sendai Bay) and December (Kasshi River and Kamaishi Bay). Temperature measurements are from the Kitakami River from 2013 to 2017, Sendai Bay (at Shiogama Bay) from 2013 to 2017, the Kasshi River from 2016 to 2017 and Kamaishi Bay from 2013 to 2017. The shaded areas indicate the interquartile ranges (dark colour) and the maximum and minimum (light colour) temperature. The histograms show the proportion of weighted average number of adults returning out of the total number of adults caught at spawning grounds in each river from 2013 to 2016 in 5 day periods. (C) Map of the downstream section of the Kitakami River, where early-run chum salmon were captured. Yellow arrowhead indicates the capture site in the Kitakami River. Coloured diamonds represent temperature-monitoring sites in the Kitakami River (light red) and Shiogama bay (dark red), which is one of the branch bays in Sendai Bay. (D) Map of the Kasshi River, where late-run chum salmon were captured. The International Coastal Research Center is where all experiments were performed. Yellow arrowhead indicates the location of the set net. Coloured diamonds represent temperature-monitoring sites in the Kasshi River (light blue) and Kamaishi Bay (dark blue).

chum salmon off the Sanriku coast show seasonal changes in their swimming behaviours (Tanaka et al., 2000). Early-run chum salmon perform repeated vertical movements in shallow water to obtain directional cues, and they also dive to cool water below the thermocline (50–180 m depths) for energy conservation by behavioural thermoregulation (Tanaka et al., 2000). Thus, the mean ambient temperature of early-run individuals ranges from 13 to 19°C (Tanaka et al., 2000). Although early-run chum salmon can buffer high SST through their vertical movements, early-run fish off the Sanriku coast nonetheless experience high water temperatures (18–20°C) at the surface (Kitagawa et al., 2016; Tanaka et al., 2000). Moreover, early-run chum salmon can encounter high water temperatures in rivers and near estuaries (Fig. 1). In contrast to early-run chum salmon, late-run chum salmon off the coast spend most of the time at the surface, and they do not perform vertical movements (Tanaka et al., 2000). It is reported that the mean ambient

temperature of late-run individuals off the coast ranges from 12 to 15°C (Tanaka et al., 2000). These differences in temperature experienced during their migrations suggest that the two populations are locally adapted to their thermal environments. In contrast to the genetically determined thermal adaptation that occurs in sockeye salmon, adjustments in thermal performance in other salmonid species are related to physiological plasticity (Anttila et al., 2014; Raby et al., 2016).

It has long been proposed that phenotypic plasticity in response to temperature, i.e. thermal acclimation (Angilletta, 2009), plays a pivotal role in adjusting thermal performance to the environment. Plasticity allows ectotherms to compensate for the thermodynamic effects of temperature on metabolism (Willmer et al., 2005). Short-term and long-term acclimation experiments indicate that some species have the capacity for complete thermal compensation of RMR, MMR and AAS over a broad temperature range (Norin et al.,

2014; Sandblom et al., 2014, 2016). Thermal compensation can help to maintain metabolic rate, even when the temperature changes. Moreover, Atlantic salmon (*Salmo salar*), generally considered to be stenotherms along with other salmonids, have a high cardiac capacity to compensate for warmer temperatures (Anttila et al., 2014). For example, there is little difference in thermal cardiac plasticity between extreme northern and southern populations, which suggests that Atlantic salmon adapt their thermal performance to the local environment via physiological plasticity (Anttila et al., 2014). Anttila et al. (2014) also proposed that the pathways for adjusting thermal performance to environmental temperatures would be linked to interspecies differences in life history (Anttila et al., 2014).

Chum salmon have a different life history from that of sockeye salmon (Salo, 1991). Chum salmon fry generally out-migrate to sea at similar times to each other (Beacham and Murray, 1986), although the spawning season runs from September to January. Furthermore, Japanese chum salmon populations use common feeding migration routes, irrespective of their origin (Honda et al., 2017; Shubin and Akinicheva, 2016; Urawa et al., 2004). This contrasts with sockeye salmon, which show various population-specific life histories and habitats (Burgner, 1991), and stronger genetic isolation (Hendry et al., 2004). The fry of sockeye salmon generally spend 1 year in a lake adjacent to the spawning ground of each population and show lake-specific physiological adaptations (Eliason et al., 2017).

Several studies on thermal performance in salmonids have reported empirical evidence of adjustment involving plastic and/or genetic physiological changes and suggested that the pathways depend on species-specific ecological contexts. However, the issue is not fully understood, and we need more detailed information, in particular, comparing thermal performance for metabolic traits among populations. Therefore, the aims of this study were to explore (1) whether early-run and late-run chum salmon have different thermal performance in their metabolic traits, and (2) the mechanistic basis underlying differences in thermal performance, if the two populations have different thermal profiles. We focused on two local populations of chum salmon obtained from the Kitakami River (early-run) and the Kasshi River (late-run) in the Sanriku coastal area (Tsukagoshi et al., 2017). The two populations differ genetically (Tsukagoshi et al., 2017) and they return to the spawning grounds in autumn and early winter, respectively (Okazaki, 1982). They also experience differences in river temperature and migration distance (Fig. 1, Table 1). In the present study, we examined the thermal performance of metabolic rates and critical temperature maxima (CT_{max}) in both populations. Based on these data, we then evaluated the thermal performance curves of AAS in both populations. In doing so, our broad objective was to compare thermal profiles in metabolic traits between the two populations, to better understand how fish adjust their thermal performance to environmental conditions.

MATERIALS AND METHODS
Animal collection and husbandry for morphological measurement
All experiments were conducted from 2015 to 2018 at the International Coastal Research Center (ICRC), Atmosphere and Ocean Research Institute, University of Tokyo (Fig. 1D). Early-run and late-run chum salmon, *Oncorhynchus keta* (Walbaum 1792), were collected in the Kitakami River and the Kasshi River, respectively (Fig. 1C,D), and transported to the ICRC. Upon arrival, fish were dip-netted from the transport tank, and then individually placed into 500 l holding tanks (diameter 1.05 m, depth 0.75 m). Before the experiment, fish were given 1–2 days to acclimate to holding tanks. We only used male fish because the absolute values of AAS are different in each sex (Clark et al., 2011). Early-run chum salmon [total *n*=20; median fork length (FL) 71.8 cm; median body mass 3.4 kg; Table 2] were caught using a dip net by fishers at Wakuya Araizeki, which is an overfall weir, approximately 35 km from the mouth of the Kyu-Kitakami River (Fig. 1C). Fish were caught from 4 to 18 October in 2016 (13.6–19.6°C) and from 7 to 15 October in 2017 (14.2–15.6°C). Fish (5–7 fish per collection) were transported for ∼2.5 h by road in a 500 l water tank (1×1×0.7 m) after each collection. Late-run chum salmon (total *n*=23; median FL 65.8 cm; median body mass 2.7 kg; Table 2) were captured using a set net, which was placed 3 km upstream of the mouth of the Kasshi River and managed by fishers. Fish were caught from 16 December 2015 to 9 January 2016 (7.0–11.5°C) and from 7 December 2017 to 9 January 2018 (7.0–12.0°C). Late-run chum salmon were individually transported for ∼30 min by road in a 250 l water tank (0.85×0.85×0.55 m) to the ICRC (Fig. 1D).

Prior to the respirometry or thermal tolerance experiments, all fish were anaesthetized using FA100 (eugenol, 107 mg ml^{-1}; Tanabe Seiyaku Co. Ltd, Osaka, Japan) at a concentration of 0.5 ml l^{-1} in holding tank water. Under anaesthesia, the fish were weighed and measured for FL. All fish were then killed using cervical dislocation and the ventricle was removed. The ventricles were blotted and weighed for relative ventricle mass (RVM). RVM was calculated using the formula RVM=0.1×(M_v/M_b), where M_v is ventricle mass (g) and M_b is body mass (kg).

A hatchery-based stock enhancement programme has been implanted in both rivers, but we have no way to distinguish hatchery-origin from wild-origin fish. All experimental procedures were in accordance with the guidelines of the Animal Ethics Committee of the University of Tokyo, and the protocols of the study were approved by the same committee (P16-7).

Temperature of the migratory environment and catch data for chum salmon
We obtained water temperature records from several difference sources. Long-term temperature records that are automatically collected from Shiogama Bay and the Kitakami River (river temperature) (Fig. 1C) by the Tohoku National Fisheries Research Institute and the Ministry of Land, Infrastructure, Transport and

Table 1. Environmental characteristics and migration difficulty indices for early-run and late-run chum salmon

Population	Capture river	Peak arrival	Migration distance (km)	Migration elevation (m)	Slope (m km^{-1})	River temperature (°C)			SST (°C)		
						10th	50th	90th	10th	50th	90th
Early-run	Kitakami River	Late October	90–200	20–130	0.20–1.25	12.3	14.5	18.3	15.5	17.5	21
Late-run	Kasshi River	Mid-December	2–4	<6	1.00–1.78	4.9	6.9	8.5	11.4	12.6	14.1

Peak spawning ground arrival time, migration distance, migration elevation and slope were estimated from catch data from hatcheries in the Kitakami River system and the Kasshi River. The 10th, 50th (median) and 90th percentiles of river and sea surface temperature (SST) are provided for October (early-run) and December (late-run).

Table 2. Median fork length, body mass and ventricle size for early-run and late-run chum salmon

Population	N	Fork length (cm)	Body mass (kg)	Ventricle size	
				Mass (mg)	RVM (%)
Early-run	20	71.8 (66.4–73.1)	3.4 (2.7–3.8)	6.8 (5.2–7.6)	0.19 (0.18–0.22)
Late-run	23	65.8 (62.0–67.7)	2.7 (2.4–3.0)	4.9 (4.1–5.8)	0.19 (0.17–0.20)

RVM, relative ventricular mass. The interquartile range is given in parentheses.

Tourism, respectively, were used for October for the early-run chum salmon. We also used long-term temperature records obtained from Kamaishi Bay (Fig. 1D), supplied by the Iwate Fisheries Technology Center, for SST in December for late-run chum salmon. As there were no data for water temperature in the Kasshi River, we collected water temperature data in the Kasshi River with a thermal logger (DEFI2-T, JFE Advantech Co., Ltd, Hyogo, Japan) from September 2016 to January 2018. The thermometer was placed approximately 4 km from the mouth of the Kasshi River, which was near to chum salmon rearing habitat. To investigate the timing of arrival of each chum salmon population at the spawning ground, we used catch data for hatcheries in each river system, provided by the Iwate Fisheries Technology Center. The catch data were collected near the spawning grounds in each river system. To estimate the average proportion of adults returning to each spawning site from the total number of adults returning, we pooled catch data from 2013 to 2016 and calculated the weighted average, because there were no differences between years in the timing of adult arrival at each spawning area.

Respirometry and swimming experiment
We used a Brett-type swim tunnel respirometer (West Japan Fluid Engineering Laboratory Co. Ltd, Nagasaki, Japan) at the ICRC to measure the rate of oxygen uptake ($\dot{M}_{O_2}$). The respirometer in the swimming section was 95 cm long, 26 cm wide and 30 cm deep. The tank in the swimming section of the respirometer held 250 l of water; water flow was generated using a voltage-controlled motor and propeller, where the voltage was calibrated against water velocity. The respirometer was sealed using an acrylic board to prevent gas exchange. Background dissolved oxygen concentration, measured when there were no fish in the swim chamber, was negligible. Dissolved oxygen concentration in the chamber was measured using a fibre optic oxygen meter with automatic temperature compensation (Firesting O_2, PyroScience GmbH, Aachen, Germany). To calculate AAS (AAS=MMR−RMR), RMR and MMR were measured in individual fish from each population at each of five test temperatures. Early-run chum salmon were assigned to 12, 14, 16, 20 or 24°C (n=3–5 per temperature), and late-run chum salmon were assigned to 8, 12, 16, 20 or 22°C (n=3–5 per temperature). We could not prepare or store water cooler than the lowest temperature (12°C in early-run and 8°C in late-run salmon), because the cooling capacity of the swim tunnel was not sufficient to stabilize the water temperatures during the experimental period. Furthermore, we were unable to maintain fish at extremely high temperatures (≥20°C) as shown in Eliason et al. (2011). Thus, we adopted an alternative method of acclimation at high water temperature based on the protocol described by Eliason et al. (2011) (details are given below).

Individual fish were acclimated to each test temperature for 1 day prior to respirometry measurements. Fish tested at 8–16°C were first given 5–8 h to adjust to the swim tunnel at a water speed of 0.3 FL s^{-1}, at which point they became calm and ceased to swim. Fish tested at 20°C or above were acclimated to the holding tank at 16°C for 1 day. The fish were then introduced into the swim tunnel,

and after 1 h acclimation the water temperature was increased by 4°C h^{-1} to the test temperature, a rate that was used in an earlier study (Eliason et al., 2011). This rate of warming might be faster than the rate at which the fish respond physiologically. However, salmon experience and tolerate equally large temperatures gradients in the wild. In addition to this, we think that salmon can respond physiologically to this rate of warming: adult sockeye salmon have shown smooth RMR curves during an acute temperature increase of 2°C h^{-1} without an acclimation period, implying that migrating salmon have considerable physiological resilience to acute temperature change (Steinhausen et al., 2008). After reaching the test temperature, fish were given 3 h to adjust to the experimental conditions at a water velocity of 0.3 FL s^{-1}. RMRs of all fish were measured after each acclimation period. The rate of oxygen uptake was measured at least three times at 0.3 FL s^{-1}, and the lowest value from the trials was used as RMR. After measuring RMR, maximal exercise was achieved using a critical swim speed (U_{crit}) test based on a protocol described previously (Makiguchi et al., 2017). Briefly, the water flow was increased to 0.9 FL s^{-1} and the fish were made to swim for 15 min. After each 15 min period, the water flow was increased by an additional 0.3 FL s^{-1} and was maintained at the new velocity for 15 min or until the fish were unable to swim against the current and were pushed to the downstream screen, and remained there for more than 10 s. As soon as the fish showed signs of fatigue (e.g. failing to maintain position in the swim tunnel or showing 'burst' swimming style), we started to measure $\dot{M}_{O_2}$. MMR was taken as the highest value obtained for any 2 min period during the swim. Once measurements of $\dot{M}_{O_2}$ were complete, fish were allowed to rest quietly for >1 h. The fish were then removed from the swim tunnel and transferred to a holding tank.

$\dot{M}_{O_2}$ was determined during the measuring period (Δt) as the decline in P_{O_2} ($\Delta|O_2|$) in the swim tunnel. $\dot{M}_{O_2}$ in mg O_2 kg^{-1} min^{-1} was calculated as:

$$\dot{M}_{O_2} = \frac{(\Delta[O_2]/\Delta t)(V_{ch} - V_b)}{M_b},\qquad(1)$$

where $[O_2]$ is the oxygen concentration (measured in mg O_2 l^{-1}), t is time (in min), V_{ch} is the volume of the swim chamber (in l), V_b is the volume of fish (in l, which was calculated from body mass assuming the density of the fish was 1 kg l^{-1}) and M_b is body mass (in kg).

CT$_{max}$ test
The thermal tolerance of fish was tested using a critical maximum temperature protocol (Anttila et al., 2013; Chen et al., 2015). Fish were kept in a holding tank for 24 h. Fish were dip-netted from the tank into a 250 l swim chamber with aerated and temperature-controlled circulating water. After a 1 h acclimation period in the test chamber at 16°C, the water temperature was increased at 4°C h^{-1} until CT$_{max}$ was reached. CT$_{max}$ was defined as the temperature at which an individual lost equilibrium continuously for 10 s. Immediately after the test, the water temperature was decreased by adding cool water (<12°C) to the test chamber until fish recovered from loss of equilibrium. After the experiment, fish were

anaesthetized in FA100 (0.5 ml l^{-1}) to measure body size and mass (see above). During the experimental test, we mixed the water in the test chamber using a flow rate of 0.3 FL s^{-1} to ensure a uniform water temperature throughout the chamber. All CT$_{max}$ tests were performed on individual fish. Water temperature was monitored using a thermometer (Firesting O$_2$, PyroScience GmbH). All fish survived testing and were subsequently killed by cervical dislocation.

Statistical analysis

All statistical analyses were conducted in R (http://www.R-project.org/). To examine the effect of population differences on the relationship between RMR and temperature, we used a generalized linear model (GLM). RMR was fitted with an exponential function, where RMR was expressed as a function of temperature. Model selection was accomplished using the Akaike information criterion (AIC), and the model with the lowest AIC was considered the most parsimonious. In addition, the likelihood ratio test was also performed. MMR was fitted with a quadratic function using minimum least squares non-linear regression. A Mann–Whitney U-test was used to compare RVM and CT$_{max}$ between the early-run and late-run chum salmon.

In order to estimate thermal performance curves of aerobic scope, the data were fitted with a two-part performance curve after Deutsch et al. (2008) and Payne et al. (2016):

$$\text{AAS}(T) = \begin{cases} S \times e^{-\left((T-T_{opt})/2\sigma\right)^2} & T \leq T_{optAAS} \\ S\left(1 - \left(\dfrac{T - T_{optAAS}}{T_{opt} - \text{CT}_{max}}\right)^2\right) & T > T_{optAAS} \end{cases}, \quad (2)$$

where AAS is absolute aerobic scope, T is temperature, T_{optAAS} is the temperature at which performance is maximized, σ is the standard deviation for the normally distributed half of the curve, CT$_{max}$ is the highest temperature at which AAS is zero and S is a scalar equal to the maxima of AAS (AAS$_{max}$). The data for CT$_{max}$ were assigned to zero for AAS. Curves were fitted using minimum least squares non-linear regression in the program R.

RESULTS

RMR and MMR

RMR was lower in early-run than in late-run chum salmon at the same temperature but increased with increasing water temperature by a similar amount in the two populations (Fig. 2A). The GLM

Table 3. Generalized linear model of the effect of independent variables on resting metabolic rate (RMR; mg O$_2$ kg^{-1} min^{-1}) in chum salmon

Parameter	Estimate		P-value
	AIC	ΔAIC	
Temperature+Population	**69.96**	0.00	<0.01
Temperature	80.09	10.13	<0.01
Null model	126.79	56.84	

A likelihood ratio test was used to test the significance of the fixed effects compared with the null model. Bold indicates a selected model.

indicated that the populations differed in their fitted curves of RMR (Table 3, Fig. 2A). The relationship between RMR and temperature (T) was explained by the equations RMR=0.707$e^{0.088T}$ for early-run chum salmon and RMR=0.915$e^{0.088T}$ for late-run chum salmon (Fig. 2A). The temperature coefficients (Q_{10}) for RMR were 2.6 ±0.5 (mean±s.d.) across the range 12–24°C in early-run chum salmon, and 2.3±0.4 across the temperature range 8–22°C in late-run chum salmon. MMR of early-run chum salmon increased with water temperature, then reached a plateau after ∼20°C. MMR of late-run chum salmon reached a maximum value around 16°C and remained at this level thereafter (Fig. 2A).

CT$_{max}$

The median CT$_{max}$ in early-run chum salmon was 27.8°C (n=4) and that of late-run chum salmon was 24.9°C (n=5; Fig. 2B). The CT$_{max}$ of early-run chum salmon was significantly higher than that of late-run chum salmon (Mann–Whitney U-test: U=0, P<0.05).

Thermal performance curve of aerobic scope

From the temperature- and population-specific patterns in RMR and MMR, T_{optAAS} for aerobic scope was 17.6°C in early-run and 14.0°C in late-run chum salmon (Fig. 3, Table 4). Both lower T_{pej} and upper T_{pej} were higher in early-run than in late-run chum salmon (Table 4). The overlap of historic river temperature and SST data with the AAS curves indicated that early-run chum salmon maintained higher metabolic performance during their migration (Fig. 3). Conversely, AAS curves for late-run chum salmon increased with river temperature, although the T_{pej} range overlapped with SST during December (Fig. 3).

Although the T_{pej} ranges of each population were different, the breadth of the T_{pej} ranges did not differ greatly (Table 4). AAS$_{max}$ did not differ between the two populations (Fig. 3, Table 4), despite differences in the migration distance and elevation (Table 1).
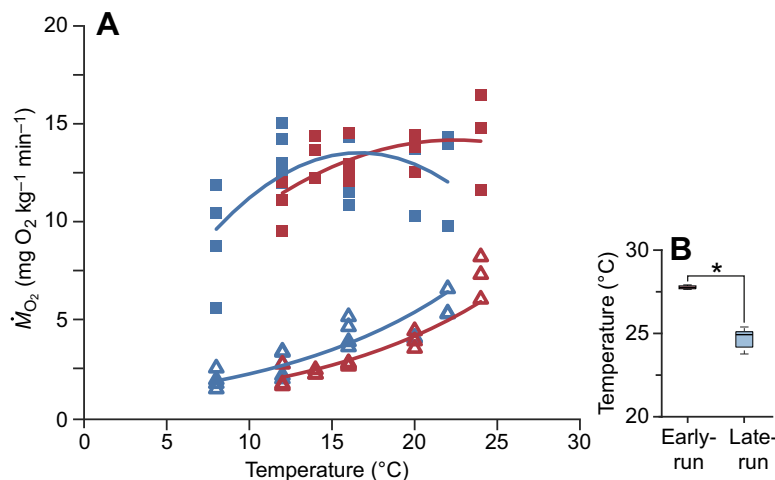

Fig. 2. Comparison of metabolic traits, and critical thermal maxima (CT$_{max}$), between early-run and late-run chum salmon. (A) Resting metabolic rate (RMR; open triangles) and maximum metabolic rate (MMR; filled squares) in early-run (red) and late-run (blue) chum salmon (early-run: n=16, late-run: n=18). Upper and lower curves indicate estimated MMR and RMR, respectively. (B) CT$_{max}$ of each population (early-run: n=4, late-run: n=5). Box plots show the median value, range, 25th and 75th percentiles, and utliers. Asterisk denotes a significant (P≤0.05) difference between populations.
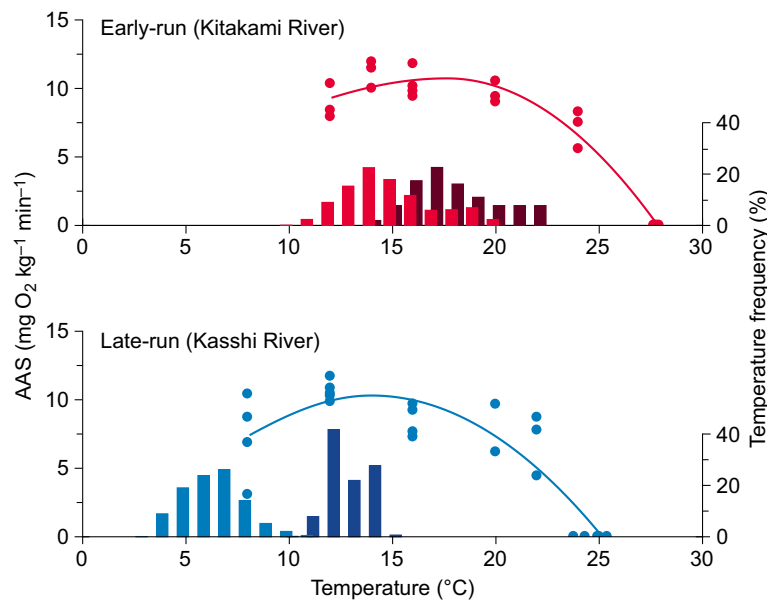
Fig. 3. Aerobic scope of early-run and late-run chum salmon. Solid lines represent a two-part performance curve fitted for each population. The data for CT_{max} were assigned to zero for absolute aerobic scope (AAS). The frequency histograms show the distribution of mean river (light red/blue) and sea surface temperatures (dark red/blue) from 2013 to 2017 in October (Kitakami River and Shiogama Bay) and December (Kamaishi Bay). Temperatures in the Kasshi River were collected from 2016 to 2017.

Metabolic traits aligned to T_{optAAS}

The populations had similar AAS curves (Fig. 3), which suggests that other metabolic traits influence the similarity of the curves. To investigate the reason for this similarity, we aligned the RMR and MMR data to T_{optAAS} within each population (thermal differences from T_{optAAS}). Following this alignment, the populations did not appear to differ in RMR or MMR (Fig. 4A). Moreover, GLM analysis showed that the populations did not differ in RMR after RMR had been aligned to T_{optAAS} (Table 5).

Factorial aerobic scope (FAS), which is the ratio of MMR to RMR, decreased with increasing water temperature. FAS in both populations decreased just as steeply below and above T_{optAAS} (Fig. 4B). Mean FAS ranged from 2.0 to 5.9 in early-run fish and 2.2 to 5.2 in late-run fish (Fig. 4B).

Ventricular mass

RVM did not differ significantly between early-run (median= 0.185%, n=20) and late-run chum salmon (0.192%, n=23) (Mann–Whitney U-test: U=195, P=0.087; Table 2).

DISCUSSION

Chum salmon have the widest geographic distribution, and are among the most abundant, of the Pacific Salmonidae (Salo, 1991). Although the thermal performance of AAS in Pacific Salmonidae has been well studied (Chen et al., 2015; Clark et al., 2011; Eliason et al., 2011; Lee et al., 2003; Raby et al., 2016), that of chum salmon remains untested because of its relatively low commercial importance in North America (Eliason and Farrell, 2016). Although chum salmon are thought to stray more than other Pacific salmon (Keefer and Caudill, 2014), the straying rate of chum salmon (0.2–5%) is

nevertheless low (Brenner et al., 2012; Fukuzawa, 2016; Keefer and Caudill, 2014). Unfortunately, no genetic markers to identify the origin of chum salmon have been created. Most of the fish used in our study probably originate from the rivers that we refer to in this study, because the straying rate in Japan has been estimated at 0.2% on average with a maximum of 2.2% (Fukuzawa, 2016). Our study is the first to document the thermal performance curves of AAS in chum salmon. Maximum values of AAS were similar between the early-run and late-run populations (10.3 and 10.7 mg O_2 min^{-1} kg^{-1}, respectively). The maximum AAS values in chum salmon were intermediate relative to those in the other Pacific salmonid species: for example, maximum AAS in Pacific salmonids ranges from 7.7 to 13.0 mg O_2 min^{-1} kg^{-1}, except for extreme values reported in pink salmon (*Oncorhynchus gorbuscha*) (male: 18.3 mg O_2 min^{-1} kg^{-1}, female: 16.3 mg O_2 min^{-1} kg^{-1}) (Clark et al., 2011). Further, the breadths of the T_{pej} range in early-run and late-run chum salmon (8.0 and 6.8°C, respectively), were similar to, or slightly wider than, the breadths of the T_{pej} range in other salmonid species (range: 3.9–8.4°C) (Chen et al., 2015; Clark et al., 2011; Eliason et al., 2011; Lee et al., 2003; Raby et al., 2016). The median CT_{max} values were 27.8 and 24.9°C in early-run and late-run chum salmon, respectively.

However, the absolute values of AAS_{max}, the breadths of the T_{pej} ranges and CT_{max} that we report may be overestimates. In pink salmon, there are sex-specific differences in maximum AAS and the breadth of the T_{pej} ranges (Clark et al., 2011). In addition, the rapid heating that we used (4°C h^{-1}) might cause our CT_{max} values to be overestimated (Terblanche et al., 2007). Nevertheless, we believe that the degree of overestimation that might have occurred in our study would not greatly affect the differences in thermal performance between the populations. This is because the direction

Table 4. Summary of two-part performance curve fitting to aerobic scope data collected from chum salmon populations

Population	T_{optAAS} (°C)	Lower T_{pej} (°C)	Upper T_{pej} (°C)	$CT_{max,pc}$ (°C)	σ (°C)	AAS_{max}	T_{pej} breadth (°C)
Early-run	17.6	12.8	20.8	27.8	7.4	10.7	8.0
Late-run	14.0	10.7	17.5	25.2	5.1	10.3	6.8

Estimates were generated from individual fish data using a two-part performance curve. Using these equations, T_{optAAS} was defined as the temperature with maximum aerobic scope, upper and lower T_{pej} were defined as the maximum and minimum temperature at which absolute aerobic scope (AAS) remained above 90% of the maximum AAS (AAS_{max}), and $CT_{max,pc}$ was defined as the maximum temperature at which AAS was zero for the performance curve.

of the observed differences was clear, and the experimental conditions (the size and sex of the fish, and heating rate used in the CT_{max} test) were similar in the two groups.

Aerobic scope and migratory environment

Oncorhynchus spp., including chum salmon, show strong fidelity to their natal streams for spawning. As *Oncorhynchus* spp. have only one opportunity to spawn, the upriver adult spawning migration is predicted to be under selective pressure. Therefore, each local population of Pacific salmonids should have a population-specific thermal performance window of AAS (Clark et al., 2011; Eliason et al., 2011, 2013; Lee et al., 2003; Raby et al., 2016). Our study revealed that the optimal thermal range of AAS in chum salmon differed between the two populations. Early-run chum salmon performed at higher temperatures than late-run salmon, and could perform at the river and sea temperatures that we measured, except for extremely high SSTs over 20°C. Early-run chum salmon off the Sanriku coast thermoregulate using vertical movements, and spend less than 15% of their time at the surface, experiencing on average a temperature range of 13–19°C (Tanaka et al., 2000); this range, which is narrower than the range of SST, is probably close to the T_{pej} range in early-run chum salmon.

Conversely, late-run chum salmon had lower T_{optAAS} than early-run salmon, and their thermal range corresponded with the seawater rather than river temperature range. This may be related to their reproductive ecology. Late-run chum salmon tend to spawn further downstream than early-run chum salmon (Salo, 1991). In particular, late-run salmon from the Sanriku coast are unusual, as their main spawning areas are located only a few kilometres upstream (Aoyama, 2017). There are not enough data about the duration of chum salmon migration in the Sanriku coast. However, late-run fish reached the spawning ground in 1 day in the Kasshi River, estimated through VHF tracking, whereas early-run fish took 1–3 weeks to travel upstream, also estimated through VHF tracking (T.K.A., T.K. and K.S., unpublished data). Previous studies have shown that the peaks of thermal performance curves in some populations do not always correspond with the mode of historically experienced temperatures (Clark et al., 2011; Eliason et al., 2013; Raby et al., 2016). These populations, which have relatively short migration distances, showed the same tendency: their AAS increased throughout historically experienced temperature. Indeed, it has been suggested that some coastal sockeye salmon populations could reach their spawning areas with relatively low MMR, and therefore low AAS, because their

Table 5. Generalized linear model of the effect of independent variables on RMR (mg O_2 kg^{-1} min^{-1}) in chum salmon, after RMR was aligned to T_{optAAS} in each population

Parameter	Estimate		P-value
	AIC	ΔAIC	
Temperature+Population	69.96	1.15	
Temperature	**68.81**	**0.00**	<0.01
Null model	126.79	57.98	

A likelihood ratio test was used to test the significance of the fixed effects compared with the null model. Bold indicates a selected model.

migration challenges are not as severe as those for upriver populations (Eliason et al., 2011, 2013; Farrell et al., 2008). Thus, late-run chum salmon may not need to maximize their aerobic performance at freshwater (river) temperatures.

The effect of salinity on the shape of AAS curves is not yet fully understood. It has been tested once, and at one temperature, in one species (sockeye salmon); AAS was found to be lower in seawater than in freshwater (Wagner et al., 2006). More research is therefore required to understand how the AAS curve changes in response to salinity.

Mechanistic basis for differences in thermal performance of metabolic traits

In this study, the RMR values for early-run chum salmon tended to be lower than those of late-run chum salmon at the same temperature. The thermal performance curve of RMR in the early-run population was shifted approximately 3°C to the right compared with that of the late-run population. The differences between the two populations in T_{optAAS}, T_{pej} range and $CT_{max,pc}$ (CT_{max} of the performance curve), which define the shape of thermal performance curves of AAS, were close to 3°C, indicating the AAS performance curves were also shifted to match these relationships. These results suggest that chum salmon adjust their thermal performance window through compensatory alteration of their metabolic traits (RMR, MMR and AAS). When the data for RMR and MMR were aligned to T_{optAAS}, it became clear that the populations did not differ in RMR and MMR (Fig. 4A). Moreover, the ratio of MMR to RMR (the FAS) was similar in the two populations when the data were aligned to T_{optAAS} (Fig. 4B), indicating compensatory alteration in metabolic traits.

Such metabolic compensatory alteration is known as thermal compensation (Willmer et al., 2005). Thermal metabolic
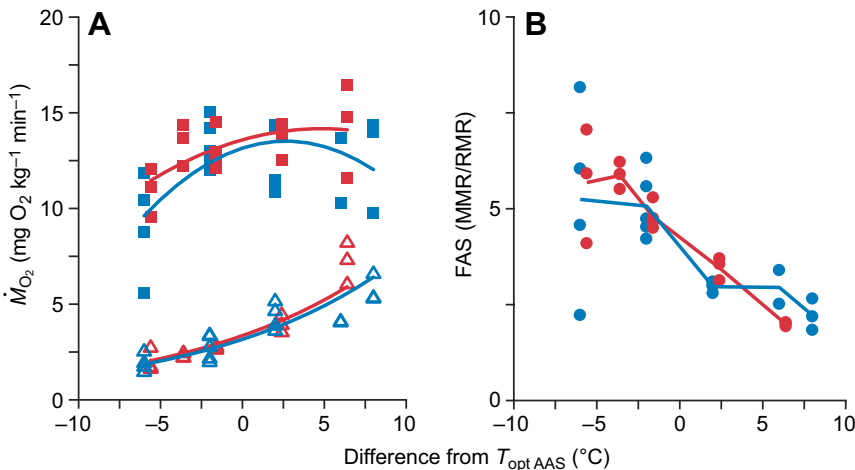

Fig. 4. Relationship between metabolic traits and the difference from optimum temperature of aerobic scope (T_{optAAS}) in chum salmon. (A) Open triangles indicate RMR of early-run (red) and late-run (blue) salmon aligned to the difference from T_{optAAS} (experimental temperature−T_{optAAS}). MMR is represented by filled red (early-run) and blue (late-run) squares. Upper and lower curves represent the fitted curves for MMR and RMR, respectively. The best GLM estimation for thermal sensitivity of RMR after the alignment was without the effect of population (see Table 5). However, even if the estimation for RMR included the effect of population, the effect was negligible. (B) Filled circles represent the factorial aerobic scope (FAS=MMR/RMR) for early-run (red) and late-run (blue) salmon and solid lines indicate the moving average of FAS for early-run (red) and late-run (blue) salmon.

compensation is fully described in the literature on thermal acclimation; that is, plasticity in response to temperature (Sandblom et al., 2014; Schmidt-Nielsen, 1997). Researchers working on Atlantic salmon have proposed that physiological plasticity could have implications for thermal accommodation in migrating salmonids (Anttila et al., 2014). Atlantic salmon from northern and southern populations show similar cardiac plasticity in response to thermal acclimation, which suggests that Atlantic salmon adjust their thermal performance to environmental temperature through thermal acclimation (Anttila et al., 2014). Interestingly, a study of two coho salmon populations (*O. kisutch*) reported that, even though the two populations had similar ecological characteristics and life histories, their thermal performance windows of AAS were different (Lee et al., 2003; Raby et al., 2016). One of the reasons for the difference might be thermal acclimation (Raby et al., 2016), as the test seasons were different (i.e. November and January versus late October and early November) and the CT_{max} values for juveniles were similar in the two populations (McGeer et al., 1991). Similarly, early-run chum salmon in the Sanriku coastal area encounter higher seawater temperatures than late-run chum salmon (Kitagawa et al., 2016; Tanaka et al., 2000). Further evidence comes from temperature profiles of mature chum salmon that were released at their feeding grounds in the Bering Sea in July, and recaptured in September or October; these profiles reveal that the chum salmon experienced low temperatures (4–9°C) at first, and a gradual increase in temperature as they approached the coast of Japan (Azumaya and Ishida, 2005; Tanaka et al., 2005). Chum salmon take 60–90 days to migrate from the Bering Sea to the coast of Japan; this is long enough to cause plastic responses in metabolic rates. Therefore, it is likely that the compensatory differences between the two populations we studied result from differences in the thermal history of the individuals, particularly differences in seawater temperatures experienced during migration.

However, the capacity to acclimate to rising temperature is itself considered to be genetic (Narum et al., 2013; Terblanche et al., 2011). Therefore, it is likely that local adaptation would have occurred in the two populations. Indeed, it has been shown in various species that ectotherms adapt locally by altering their potential for thermal tolerance (e.g. common killifish, *Fundulus heteroclitus*: Fangue et al., 2006; Atlantic cod, *Gadus morhua*: Lucassen et al., 2006; and rainbow trout, *Oncorhynchus mykiss*: Chen et al., 2015, 2018; Narum et al., 2013). Moreover, through genetic adaptation, some species of Pacific salmon alter their thermal performance curves (Chen et al., 2018; Eliason et al., 2011). In such cases, the thermal performance improves because cardiac function is protected at temperature extremes, enabling more oxygen to be delivered to internal tissues; thermal performance does not arise from a compensatory thermodynamic effect on metabolism (Chen et al., 2018; Eliason et al., 2011). In fact, it would appear that the changes in the shape of the MMR curves (caused by breathing) mainly affected thermal performance (Chen et al., 2018; Eliason et al., 2011). Those results differ from the population differences that we observed in chum salmon, in that the RMR and MMR curves in our study were shifted. Therefore, if the two chum salmon populations that we studied adapt locally to environmental temperature, it is likely that early-run chum salmon have a greater, or simply different, capacity for thermal acclimation than the late-run chum salmon, rather than a greater capacity to deliver oxygen to internal tissues, as occurs in sockeye salmon and redband trout (a subspecies of rainbow trout) (Chen et al., 2018; Eliason et al., 2011). Unfortunately, it is difficult to acclimate adult chum salmon to new temperatures, because they die within 1–3 weeks of entering freshwater rivers. Thus, we cannot evaluate the effect of genetic

differences on thermal performance in chum salmon. Nonetheless, our results, which reveal that the sensitivities of metabolic rates can shift, imply that a plastic response of metabolic rates would enable the thermal performance window to adjust to environmental temperatures. Further investigation using other life stages and approaches is required to understand how genetic differences affect thermal plasticity in chum salmon and, specifically, the implication that genetic and/or plastic factors determine thermal performance.

The pattern of thermal accommodation to environmental temperatures observed in chum salmon differs from the apparently strong local genetic adaptations of sockeye salmon. The populations of chum salmon that we studied showed similar thermal performance curve shapes. In contrast, various shapes of thermal performance curves (with different peaks and breadths) have been reported for sockeye salmon (Eliason et al., 2011). Interspecies differences in life history would be linked to differences in the type of thermal accommodation. Sockeye salmon show considerable diversity in life history and in the timing and distance of upriver migration (summer versus autumn: 120–1070 km), elevation (10–1174 m) and temperature (11–18°C) (Eliason et al., 2011). In contrast, the upriver migration conditions experienced by chum salmon in our study did not differ greatly between the populations (Table 1), compared with the large differences in upriver migration conditions reported for sockeye salmon populations. Further, unlike those of sockeye salmon, chum salmon spawning sites occur mostly in lower to middle river basins and in river mainstreams. In addition, the strong spawning site fidelity of sockeye salmon contrasts with the lower fidelity of chum salmon (Brenner et al., 2012; Fukuzawa, 2016; Keefer and Caudill, 2014). Because chum salmon experience less diverse upriver migration conditions and stray more, they might experience less selective pressure than sockeye salmon, resulting in the similar shapes of the thermal performance curves that we observed.

Ecological implications for thermal compensation of metabolic traits

It has been proposed that ectotherms can compensate for temperature change through plastic (physiological), genetic and behavioural responses (Farrell, 2016). Behavioural compensatory responses thorough vertical movements have been observed in chum salmon migrating off the Sanriku coast (Tanaka et al., 2000). Our results add to this evidence, by revealing that metabolic thermal compensation in early-run chum salmon contributed to maintaining their thermal performance. Our results also indicate the potential benefits of thermal compensation in lowering the costs of migration.

Chum salmon usually stop feeding when they start their upriver migration (Hasler et al., 1978). Thus, it is important for chum salmon to reduce migration costs, because they must complete their spawning migration using the energy reserves stored in their body (Tanaka et al., 2000). Early-run chum salmon experience higher water temperatures during their migration than late-run salmon, which migrate in winter. Previous studies showed that early-run chum salmon migrating in coastal areas move vertically within the water column and use the cool mass below the thermocline as a thermal refuge (Tanaka et al., 2000), and other salmonids have also shown this behaviour (Newell and Quinn, 2005). The function of this behaviour is considered to be thermoregulation to conserve energy. However, the running waters of a river are usually mixed, so that strong vertical gradients in water temperature do not develop. Moreover, early-run chum salmon off the Sanriku coast cannot always use thermal refugia below the thermocline; for example, when the thermocline is disrupted by wave stirring action caused by

atmospheric depression. In this situation, early-run chum salmon eventually stop seeking a thermal refuge and remain at the surface (Kitagawa et al., 2016). Therefore, under certain circumstances, chum salmon may not be able to regulate their body temperature using a thermal refuge, whether they are in rivers or coastal regions. Instead, thermal compensation for RMR would play a pivotal role in minimizing the cost of migration in high water temperature conditions.

Global climate change is currently a controversial topic in the study of aquatic ectotherms (Pörtner and Farrell, 2008). Unusually high water temperatures have a negative effect on migrating salmonids; this has been observed as high *en route* migration mortality in sockeye salmon in response to high temperature (Farrell et al., 2008). The highest water temperature experienced by early-run chum salmon in our study during their upstream migration was approximately 20°C. At this temperature, early-run chum salmon can perform at 95% of AAS_{max}. With a further increase of 2–4°C, early-run fish will experience worse metabolic performance during upriver migration (82% and 61% of AAS_{max} at 22 and 24°C, respectively), in the absence of plastic and/or genetic physiological changes. Although the same is true for late-run chum salmon, they do not reach AAS_{max} under the river temperatures that they experience (40–86% of AAS_{max} at 4–10°C), suggesting that warming water temperature could improve their metabolic performance. The metabolic adjustments (in AAS) that are required to complete spawning migration are still poorly understood. Biologging and biotelemetry technologies play a key role in this research, as demonstrated for Fraser River sockeye salmon (Farrell et al., 2008). Further, these techniques have potential for evaluating the higher energetic costs associated with rising water temperature, which will help in understanding the effect of global warming on aquatic ectotherms.

Conclusions and perspectives
On the Sanriku coast, early-run and late-run chum salmon return to spawn in different thermal environments. Our results showed that the populations had different thermal performance curves for AAS, confirming our expectations. The mechanistic basis for the difference resulted from compensatory alteration of metabolic traits, implying that plasticity of metabolic pathways would require thermal accommodation in chum salmon. However, further study is needed concerning local adaptation in chum salmon – specifically, the effect of population differences on the potential for thermal tolerance. The thermal accommodation characteristics of the populations that we studied may be related to ecological conditions, the location of the spawning site (lower or middle river basin) and spawning ground fidelity. Our study provides a new perspective on the metabolic adjustments of fish to thermal regimes. Further investigation is needed to better understand the evolutionary factors leading to the various pathways of thermal accommodation.

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