The Ecological Context of Aerobic Scope in Cost of Transport for Chum Salmon Migrating Upriver

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Ectotherms adjust their thermal performances to various thermal ranges by altering their metabolic rates (Angilletta 2009). Exploring the relationship between thermal niche and the performance of metabolic traits is a controversial topic in the thermal adaptation of ectotherms. Aerobic scope (AS), the difference between resting metabolic rate (RMR) and maximum (aerobic) metabolic rate (MMR), has been proposed as a functional metric for thermal performance (Pörtner and Farrell 2008). The thermal sensitivity of AS is described by the thermal performance curve, where AS increases with temperature up to a peak (which is defined as the optimum temperature of aerobic scope, T_{optAS}), and declines thereafter (Payne et al. 2016). Sub-optimal temperatures are known as pejus temperatures (T_{pej}). It has been reported that some salmonid species exhibit a variety of thermal profiles for AS curves, and the thermal performance curve of each species or population roughly corresponds to their temperature regime (Lee et al. 2003; Eliason et al. 2011; Clark et al. 2011; Eliason et al. 2013; Raby et al. 2016). Although the intra- or inter-specific adaptation of AS has been shown, however, the degree of correspondence between the thermal performance curves and temperature regimes varies in species or populations. For instance, 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; Abe et al. 2019). While the studies of thermal performance curves of AS in Pacific salmonids indicated AS is an ecologically relevant trait, the ecological contexts of AS are not fully understood.

In order to explore the ecological meaning of thermal performance for AS, we used the framework of cost of transport (*COT*) with aerobic power constraint. This model incorporates the effect of maximum sustained speed (critical swim speed, U_{crit}) and the recovery time on *COT* by assuming the constraint of metabolic power supply (critical power P_{crit}) (Martin et al. 2015). The *COT* model, in other words, enables us to discuss the cost of resting and the time limitation of exercise in high-intensity swimming of salmon, which the existing *COT* model could not access.

COT ($J \cdot m^{-1} \cdot kg^{-1}$) is generally expressed as the amount of energy consumption per unit distance travelled:

$$COT = \frac{P_{travel}}{U_{swim} - U_{flow}}, \quad (1)$$

where, P_{travel} is total power spent on travel ($J \cdot kg^{-1} \cdot s^{-1}$). U_{swim} and U_{flow} are the swim speed of fish ($m \cdot s^{-1}$) and the flow speed against fish swimming direction ($m \cdot s^{-1}$), respectively. Thus, $U_{swim} - U_{flow}$ is considered as substantial migration speed. *COT* assumes a U-shaped relationship with U_{swim} , and then, the optimum swim speed U_{opt} is estimated from the *COT* curve as the swim speed, where the *COT* was minimized (COT_{min}).

P_{total} is the sum of the power requirements of maintenance metabolism P_{metb} and of swimming P_{swim} :

$$P_{total} = P_{metb} + P_{swim}. \quad (2)$$

P_{total} is equal to P_{travel} in the *COT* model without aerobic power constraint but not always equal to P_{travel} in the *COT* model with the power constraint. In the *COT* model of the present study, critical power P_{crit} was assumed, which is defined by the maximum rate of aerobic energy supply and U_{crit} was also assumed as the swim speed, where P_{total} is equal to P_{crit} . Demand for power exceeding P_{crit} is supplied from anaerobic metabolism, which has a finite capacity. Thus, in the case that fish swim over P_{crit} , the time duration of swimming was limited and the fish needed rest after exhausting anaerobic metabolism.

When fish swim under the intensity of P_{crit} , the total power requirement, P_{travel} , of migrating fish is equal to P_{total} . Meanwhile, in the case that fish swim over P_{crit} , the additional costs should be added to P_{travel} . Therefore, the *COT* model is considered as follows,

$$COT = \begin{cases} \frac{P_{total}}{U_{swim} - U_{flow}} & (P_{total} \leq P_{crit}) \\ \frac{P_{total} + P_{metb} \left[\frac{y_r(P_{total} - P_{crit})}{P_{crit} - P_{metb}} \right] + (y_r - 1)(P_{total} - P_{crit})}{U_{swim} - U_{flow}} & (P_{total} > P_{crit}) \end{cases}, \quad (3)$$

where, y_r is the recovery yield to restore substrate of anaerobic metabolism. $P_{metb}[y_r(P_{total} - P_{crit})/(P_{crit} - P_{metb})]$ is the energy expenditure during the resting period and $(y_r - 1)(P_{total} - P_{crit})$ is the overhead cost to convert a substrate, such as amino acid or lipid, to the substrate of anaerobic metabolism (e.g., glycogen). The parameters in the COT model were used from published respiration data sets (Abe et al. 2019) and estimated parameters (Martin et al. 2015).

Fig. 1. Aerobic scope of chum salmon in the Kitakami River and environmental temperature. Solid line represents a thermal performance curve fitted for salmon captured in the Kitakami River. The dashed vertical line represents the optimal temperature of AS (T_{optAS}). The histogram shows the distribution of river temperature from 2013 to 2017 in October, the seasonal timing of chum salmon return in the river.

Fig. 2. Swimming model and simulation and predicted optimal swimming behavior. (A) COT as a function of the speed the fish swims at T_{optAS} . The color indicates flow velocity. Filled circles denote the COT minimizing swim speed at each flow velocity. (B) Estimated U_{opt} and time proportion of resting under as a function of flow speed.

This COT model was applied to chum salmon (*Oncorhynchus keta*) migrating upriver in the Kitakami River because their population has a measured performance of AS and the salmon experienced temperatures below T_{optAS} throughout most of their upriver migration (Abe et al. 2019) (Fig. 1). In the COT model, fish minimize COT by swimming more rapidly through higher flow speed (Fig. 2A). The predicted behavioral response of fish to intermediate flow speed is to cap swimming speed so that power requirements do not exceed U_{crit} , but under high flow speed, U_{opt} is higher than U_{crit} (Fig. 2B). To evaluate the validity of the predicted behavior, we compared the swimming behavior of the chum salmon tagged with accelerometers to the predicted behavior. The swimming behavior of tagged chum salmon altered while migrating upriver (Fig. 3). The fish continuously swam in the lower basin, where flow speed was low, but the fish started to rest occasionally after narrowing, where flow speed starts to increase (Fig. 3B). The fraction of time spent at high swim speed also increased (Fig. 3C).

In order to examine the temperature range for minimizing COT , minimum COT (COT_{min}) was calculated for different temperature and flow speed conditions. In the case of a warmer temperature than T_{optAS} , COT_{min} were higher than T_{optAS} in any flow speed (Fig. 4A). COT_{min} sharply increased at high flow speed and warm temperature further magnified the effect of flow speed (Fig. 4A). In contrast, the simulation in lower temperature than T_{optAS} suggested the temperature minimizing COT_{min} (T_{COTmin}) was not always the lowest temperature and T_{COTmin} depended on flow speed (Fig. 4B).

The relationship between COT_{min} and water temperature for each velocity condition showed that the slower the flow speed condition, the lower T_{COTmin} (Fig. 5). T_{COTmin} approached optimal temperature as flow speed increased but did not exceed T_{optAS} in low flow speeds ($< 0.9 \text{ m}\cdot\text{s}^{-1}$) (Fig. 5). At high flow speed ($\geq 1.0 \text{ m}\cdot\text{s}^{-1}$), however, T_{COTmin} switched to moving away from T_{optAS} . Interestingly, from intermediate flow speeds ($\geq 0.7 \text{ m}\cdot\text{s}^{-1}$), COT_{min} decreased with the temperature when approaching T_{optAS} , but increased sharply after T_{optAS} . The sharp increase in COT_{min} became more remarkable with higher flow speed (Fig. 5). This is because the swim speed minimizing COT_{min} becomes higher than U_{crit} under high flow speed and chum salmon would have to spend a large fraction of its time resting. The simulation suggested that the temperature slightly below T_{optAS} minimized COT under high flow speed, that is, the temperature range is better to save COT for salmon migrating upriver. In addition, the temperature range minimizing COT_{min} corresponded to the empirical temperature of tagged chum salmon migrating upriver (Fig. 5). Our results provided a new perspective on the ecological meaning of aerobic scope. Further quantitative study is needed to better understand the metabolic adaptation of fish to thermal regimes.

Fig. 3. Study map, the distributions of flow velocity, and the swimming behavior of tagged salmon migrating upriver. (A) Study map of the tracking survey. Filled yellow and black circles represent the release point of tagged fish and the point positioned by VHF tracking, respectively. The time-series data retrieved from the attached accelerometer was classified with six sections divided by the positions. (B) The measurement of flow speed was performed at four bridges (Chitose, Hanafuji, Maiya, and Tome represented in (A)). The colors represent flow velocity and the filled circles indicate the measured values with a flow meter. Colored meshes were created using two-dimensional linear interpolation. (C) Time proportion of time occupied by high-intensity swimming inactive phase (red) and time proportion of time occupied by total time (grey) in each section.

Fig. 4. Minimum COT (COT_{min}) as a function of flow speed. The upper (A) and lower (B) figures represent the predictions of COT_{min} over and under T_{optAS} , respectively. The colored lines indicate predicted COT_{min} in each temperature. The black lines denote predicted COT_{min} at T_{optAS} .

Fig. 5. Minimum COT (COT_{min}) as a function of temperature. Colored lines indicate predicted COT_{min} in each flow speed. Filled circles denote the COT_{min} minimizing temperature (T_{COTmin}) at each flow speed. The vertical black line represents T_{optAS} . The shaded area indicates the T_{pej} range (sub-optimal temperature range). The grey lines indicate the temperatures at which AS becomes 80% of its maximum value. Box plot denotes the experienced temperatures of tagged salmon.

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