比較は、カムサケとマスサケの泳ぎの能力及び上流漂流行動の違いについて検討した。カムサケとマスサケの泳ぎの能力及び上流漂流行動の違いについて検討した。
Comparison of the swimming ability and upstream-migration behavior between chum salmon and masu salmon

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Abstract: The spawning ground of chum salmon (*Oncorhynchus keta*) is usually located farther downriver than that of masu salmon (*O. masou*) in Hokkaido, Japan. To compare the swimming abilities of these two species, the relationship between swimming speed and oxygen consumption was compared using a swim tunnel in the laboratory. Then, the upstream-migration behaviors of chum and masu salmon were compared using electromyogram (EMG) telemetry at fish passages in the Toyohira River, Hokkaido. In the laboratory study, the standard metabolic rate of masu salmon was lower and the critical swimming speed ($U_{crit}$) was faster than those of chum salmon. In the field study, the holding time needed to recover the swimming performance exceeding $U_{crit}$ at the fish passages, and the trial number needed to pass the fish passages were significantly lower for masu salmon than chum salmon. These results revealed that masu salmon are more adaptable to extended swimming in high-water-velocity conditions than chum salmon and that masu salmon are better equipped for a long distance upstream to their spawning ground than chum salmon.

**Keywords:** swimming ability; upstream-migration behavior; standard metabolic rate; critical swimming speed; fish passage; chum salmon; masu salmon.
**Introduction**

Semelparous Pacific salmon must migrate upstream with limited energy stores to reach their spawning ground, and the metabolic energy use involved in swimming ability is important for their upstream migration. The relationships between metabolic traits and swimming performance in salmon have been investigated previously. Gamperl et al. (2002) showed that wild rainbow trout (*Oncorhynchus mykiss*) exhibit aerobic fitness of at least one-third greater than that of hatchery-raised individuals. Lee et al. (2003b) suggested that the heightened aerobic fitness might be related to natural experiences during exercise. Wagner et al. (2006) investigated the differences in routine and active metabolic rates for sexually maturing migratory adult sockeye salmon (*O. nerka*) that were intercepted in the ocean and then held in either seawater or freshwater, suggesting that some of the metabolic costs might change during the migration from seawater to freshwater.

The upstream migration of salmon is energetically demanding because the fish must pass a variety of natural and anthropogenic barriers, such as waterfalls, rapidly flowing water, weirs, hydroelectric facilities, and ground sills in their natal rivers (Pon et al. 2006; 2009a, b). Specifically anthropogenic barriers have brought serious problems during the upstream migration of anadromous salmon. The upstream
spawning migration of sockeye salmon in the Fraser River, British Columbia, Canada, has been extensively examined (Hinch et al. 1996; Hinch and Rand 1998; Hinch and Bratty 2000), and many physiological data have been reported: the average swimming activity of sockeye salmon passing through Hell’s Gate were higher than at any other location in the Fraser Canyon and non-aerobic swimming performance exceeding critical swimming speed \( (U_{\text{crit}}) \) had to be sustained over a long period of time. Roscoe and Hinch (2010) reported that these barriers impede or hinder the spawning-migration routes of salmon and result in reduced salmon populations. In response, a large number of fish passages have been installed all over the world. The recent rapid development of radio telemetry technology and methods make it possible to observe the upstream-migration behavior of salmon (Cooke et al. 2004). Fish telemetry with integrated muscle electromyogram (EMG) has been used to examine the upstream migration of sockeye salmon (Hinch et al. 1996; Hinch & Bratty, 2000; Pon et al. 2009a, b). EMG can be used directly as an indicator of the intensity of fish muscle activity and to evaluate the efficiency of fish passage in relation to the swimming performance of Pacific salmon (Roscoe and Hinch 2010; Makiguchi et al. 2011).

In Hokkaido, Japan, the spawning seasons of chum salmon \( (O.\ keta) \) and masu
salmon (*O. masou*) are nearly identical, but there are many differences in their upstream spawning migrations. Masu salmon enter their natal river between April and June and then migrate upstream to the spawning ground near the riverhead in September, possibly triggered by the swollen autumnal river (Kato 1991; Mayama 1992). In contrast, chum salmon begin upstream migration between September and October and quickly reach the spawning ground in the middle reaches of the river (Salo 1991). We hypothesized that differences in swimming ability might shape the different upstream-migration behaviors of chum and masu salmon; however, to date, no study has examined the relationship between swimming ability in the laboratory and upstream-migration behavior in the field using chum and masu salmon.

The purposes of this study were (1) to examine the relationship between swimming speed and oxygen consumption, and compare swimming abilities of chum and masu salmon in a swim tunnel in the laboratory using $U_{cm}$, standard metabolic rate (SMR), active metabolic rate (AMR), and aerobic metabolic scope (AMS); (2) to investigate the upstream-migration behaviors of chum and masu salmon in the field using EMG telemetry to compare their behaviors at the fish passages in protection beds and groundsills in the Toyohira River; and (3) to discuss their upstream spawning-migration behavior in terms of metabolic energy use and swimming ability.
Materials and Methods

1) Swimming abilities in the laboratory

Experimental animals

Adult chum salmon (3 males and 2 females; mean ± SE: fork length: 62.1 ± 4.9 cm; body weight: 1.9 ± 0.7 kg) and adult masu salmon (6 males and 5 females; fork length: 53.3 ± 13.4 cm; body weight: 1.7 ± 1.4 kg) were captured using a waterwheel located approximately 70 km from the Chitose River mouth in the upper reaches of the Ishikari River in western Hokkaido, Japan, during their upstream spawning migration (Fig 1A).

Experiments were conducted at the Chitose Salmon Aquarium in September and December of 2010 and 2011. Fish were individually transferred to a compact water tank (L × W × H = 1.8 × 0.9 × 0.6 m) in an artificially flowing stream using water from the Chitose River.

Swim tunnel and swimming test protocol

A swim tunnel (West Japan Fluid Engineering Laboratory Co. Ltd, Nagasaki, Japan) was used to measure critical swimming speed ($U_{crit}$) and dissolved oxygen consumption. Water flow was generated using a voltage-controlled motor and propeller, with the voltage calibrated against the flow velocity. The swim tunnel was sealed with
an acrylic board so that no gas exchange occurred, and water from the Chitose River was pumped into it before the $U_{\text{crit}}$ trial. The water temperature ranged from 12.0 to 13.5°C and did not vary more than 1°C during any experiments.

Fish were individually placed into the swimming chamber of the swim tunnel. In all cases, fish were acclimated for 1 hour at 0.25 body lengths (BL) s$^{-1}$ to minimize handling effects before all $U_{\text{crit}}$ trials. After each 15-min period, the water velocity was increased by an additional 0.25 BL s$^{-1}$ and was maintained at the new speed for 15 min until the fish became fatigued or was unable to swim against the current. After the $U_{\text{crit}}$ trial was completed, body mass and fork length were measured. Flow-velocity values were corrected to account for solid blocking effects (Gehrke et al. 1990), as described by Bell and Terhune (1970).

The $U_{\text{crit}}$ (BL s$^{-1}$) was calculated with Brett’s formula (1964):

$$U_{\text{crit}} = U_i + (t \cdot t_i^{-1}) \cdot U$$ (1)

where $U_i$ (BL s$^{-1}$) is the highest velocity maintained for the entire swimming period; $t_i$ is the prescribed swimming period (i.e., 15 min); $t$ (min) is the amount of time spent at the fatigue velocity; and $U$ is the velocity increment (i.e., 0.25 BL s$^{-1}$).

To measure oxygen consumption (MO$_2$) during the acclimatization period and during the $U_{\text{crit}}$ trials, the oxygen concentration in the swim tunnel was measured.
throughout the trial at 1-min intervals using a multi-water-quality sensor probe (U-50; Horiba Ltd., Kyoto, Japan), which was housed inside the swim tunnel. Before the fish were introduced, air bubbles were removed from the swim tunnel. Prior to each \( U_{\text{crit}} \) trial, oxygen levels in the tunnel were reset by pumping fresh river water into the tunnel. The \( MO_2 \) per 15-min period for each fish was calculated by subtracting the quantity of oxygen at the end from the starting value. The \( MO_2 \) rate (mg O\(_2\) kg\(^{-1}\) h\(^{-1}\)) for individual fish during a velocity increment was calculated as:

\[
MO_2 = [O_2] \frac{v}{m} \tag{2}
\]

where the rate of oxygen concentration \([O_2]\) is measured in mg O\(_2\) per l\(^{-1}\) h\(^{-1}\), \( v \) is the water volume of the swim chamber (l); and \( m \) is the body mass of the fish (kg). \( MO_2 \) was then standardized to a value corrected for a fish of 1 kg (\( MO_{2\text{cor}} \)), using the following allometric relationship derived by Schurmann and Steffensen (1997):

\[
MO_{2\text{cor}} = MO_{2\text{meas}} \left( \frac{w}{w_{\text{cor}}} \right)^{(1-A)} \tag{3}
\]

where \( MO_{2\text{meas}} \) is the \( MO_2 \) measured during the trial; \( w \) is the mass of the fish; and \( w_{\text{cor}} \) is the standard body mass of 1 kg. \( A \) is the condition factor [weight (g) / length\(^3\)(cm)•100], calculated using the mean fork length and bodyweight for each species.

Standard metabolic rate (SMR) is defined as the \( MO_2 \) at zero activity (Fry 1971;
Claireaux et al. 2006; Luna-Acosta et al. 2011). Because $MO_2$ was expected to increase exponentially with swimming speed (Brett 1964), a curve was fitted for each individual, according to the following equation:

$$MO_{2\text{cor}} = SMR \cdot \exp^{bU} \ (4)$$

where $MO_{2\text{cor}}$ is the oxygen consumption obtained from (3); SMR is the standard metabolic rate that corresponds to the intercept (i.e., the $MO_2$ when $U = 0 \ \text{BL s}^{-1}$); $U$ is the swimming speed (in BL s$^{-1}$); and $b$ is a constant.

The active metabolic rate (AMR) of the fish was estimated as the maximum $MO_2$ recorded during the swimming test (i.e., when swimming speed was close to $U_{\text{crit}}$), and AMS (aerobic metabolic scope) was calculated as follows (Fry 1971):

$$AMS = AMR - SMR \ (5)$$

The net cost of transport ($COT_{\text{net}}$; mgO$_2$ kg$^{-1}$ m$^{-1}$) was calculated as follows for each swimming speed:

$$COT_{\text{net}} = \frac{MO_{2\text{net}}}{U} \ (6)$$

where $U$ is the swimming speed (m h$^{-1}$) and $MO_{2\text{net}}$ is equal to the MO$_2$ at the considered swimming speed minus SMR. AMR, SMR, AMS and $COT_{\text{net}}$ values were determined for each fish.
2) Upstream migration behavior in the field

Study area

The Toyohira River in Hokkaido, Japan, which flows through the city of Sapporo, is a rare rapid-flow urban river and an important spawning ground for chum and masu salmon. Six cross-river constructions (#1, #3-8), called groundsills, were constructed to prevent the lowering of the riverbed, and fish passages were built at each groundsill (Fig. 1B). A protection bed was also constructed at the groundsill #5, and a fish passage was installed in March 2010 (Fig. 2). Makiguchi et al. (2011) reported the effects of groundsills on the upstream migration of chum salmon in 2008 and 2009 using EMG telemetry; however, the Toyohira River environment changed significantly after their investigation; the fish passage was established in protection bed #5 in 2010, and a severe typhoon hit near Sapporo City in September 2011. In the protection bed #5, a large part of the passage was filled by a sandbar because of the change in water flow and current caused by the typhoon.

Experimental animals and transmitter attachment procedures

In the Toyohira River, adult chum and masu salmon migrate upstream from September to October. All chum and masu salmon used in this study were captured using a net 11.5-16.5 km from the mouth of the Toyohira River and transferred to
outdoor tanks at the Chitose Salmon Aquarium for calibration of the EMG signals to swimming speeds. In 2010, 3 males (fork length, 56.4–74.1 cm; body weight 1.8–4.2 kg) and 3 females (fork length, 62.6–73.5 cm; body weight 2.7–3.9 kg) chum salmon, and 3 males (fork length, 44.3–55.1 cm; body weight 0.9–1.8 kg) and 3 females (fork length, 51.0–58.6 cm; body weight 1.5–2.5 kg) masu salmon were studied. In 2011, 1 male (fork length, 68.7 cm; body weight 3.3 kg) and 5 females (fork length, 54.6–69.5 cm; body weight 1.4–3.4 kg) chum salmon, and 2 males (fork length, 53.2–56.5 cm; body weight 1.6–1.7 kg) and 1 female (fork length, 58.7 cm; body weight 2.6 kg) masu salmon were studied.

Each fish was equipped with a cylindrical, epoxy-encased EMG transmitter (CEMG-R11-35, Lotek Engineering Inc., Newmarket, Ontario, Canada; 18.3 g in air, 16.2 mm in diameter, and 53.0 mm in length) attached externally to the body surface and positioned in front of the dorsal fin using the procedure developed by Makiguchi et al. (2011). External attachment is suitable for short-term telemetry research, which reduces handling stress for the fish (Bridger and Booth 2003; Makiguchi et al. 2007). To attach the tag, experimental fish were anaesthetized using FA100 (eugenol; Tanabe Seiyaku Co. Ltd, Osaka, Japan) at a concentration of 0.5 ml l⁻¹ in water from the Chitose River and placed upright on a surgical table. Their gills were irrigated with
water containing diluted FA100 to maintain sedation during the attachment procedure.

Two stainless-steel needles large enough hold the restraining nylon ties were pushed through the dorsal muscle to secure the EMG transmitter and sutured into place using nylon ties and epoxy resin. Silicon pads were attached to minimize abrasion. The nylon ties were passed through the needles and tied on the opposite side (Bridger and Booth 2003). The EMG transmitters consisted of an epoxy-coated transmitter package with a pair of Teflon-coated electrodes with brass muscle-anchoring tips (dimension 5 × 1 mm). The EMG electrodes were inserted subcutaneously using a hypodermic needle at a ratio to the body length of approximately 0.7 on the left side of the fish. The electrodes detected electrical potentials within the axial dark muscle, which contained red muscle tissue. The amplitude and frequency of these pulses was directly correlated to the level of muscle activity. Paired electrode tips were positioned approximately 1 cm apart and secured in the lateral red muscle toward the rear of the fish. These muscles are primarily used in steady, non-bursting, aerobic swimming activity (Beddow and McKinley 1999). EMG signals are generally related to swimming speed (Økland et al. 1997). The electrodes were sutured to avoid entangling vegetation or other environmental structures.

The CEMG model was equipped with a differential muscle probe, a signal conditioning circuit, a digitizer, a microcontroller, and a radio transmitter. The voltage corresponding
to muscle activity was sampled at 2-s intervals. Individual samples were summed and stored temporarily. At the end of the interval, the mean value was calculated, and an activity level (EMG signal) ranging from 0 to 50 (no units) was assigned, and transmitted to a radio receiver (model SRX_600; Lotek Engineering Inc.). The attachment procedures usually required approximately 5 min to complete.

**Calibration of EMG signals to swimming speeds**

EMG signals were calibrated to swimming speed in the swim tunnel using procedures developed by Makiguchi et al. (2011). The Chitose River water was poured into the swim tunnel before each trial. The water temperature was set between 11.5 and 14.5°C, which was similar to the water temperature at the capture point in the Toyohira River. Experimental fish were individually placed into the swimming section of the swim tunnel, and 10 EMG signals at 0 m s\(^{-1}\) were measured using the EMG radio receiver when the fish maintained a holding position. Next, the trial was started at 0.3 m s\(^{-1}\), and the water velocity was increased incrementally by 0.3 m s\(^{-1}\), with 10 EMG signals measured at each increment. Fish readily swam against the current and rarely came in contact with the grid at the back of the swim chamber. The trial ended at 1.2 m s\(^{-1}\). We used the average EMG output at each velocity for each fish to calibrate transmitter output to swimming speed. We evaluated the relationship between the mean
EMG output and water velocity using a linear regression analysis.

**Field Study**

Few studies report that fish with EMG transmitters were calibrated in respirometers prior to their release. In September and October of 2010 and 2011, chum and masu salmon used in the EMG-calibration experiment were individually released in the study area and tracked on foot during upstream migration using a hand-held directional Yagi antenna (Table 1). The position of each individual was determined using EMG-transmitter signals received by three SRX_600 radio receivers. The radio receivers recorded EMG signals at 2-s intervals. Migration time in each segment was measured for each fish by subtracting the time on reaching the exit from the time at entry. The chum and masu salmon were often observed to have stopped swimming during their upstream migration, and more than 3 min of swimming cessation during upstream migration was defined as holding behavior. The calculation of swimming time did not include holding time. EMG signals were converted to swimming speed using the equations established from the EMG calibration for each fish. After tracking, water depth was measured at 0.2-m intervals in the water column, and water velocity was measured at 2–5-m intervals along the tracking area. All tagged fish were released below protection bed #5, and the tagged fish were tracked intermittently for
approximately 2–5 days. The number of times the fish exceeded $U_{\text{crit}}$ and the time spent swimming over $U_{\text{crit}}$ were calculated from the time-course trajectory of swim speed, using the $U_{\text{crit}}$ calculated in the laboratory for both species.

**Statistical analyses**

An analysis of covariance (ANCOVA) was used to compare the swimming abilities of chum and masu salmon in the laboratory, and separate predictive relationships were required for body length and body mass. ANCOVA was also used to compare the swimming abilities of male and female in masu salmon in the laboratory. If the ANCOVA was not be applicable in the statistical analysis, Student’s t-test was used.

Statistical comparisons of the swimming performance of chum and masu salmon in the field were analyzed using Student’s t-test. The results were expressed as the mean ± SE, and data were considered significant when $P < 0.05$.

For the relationship between swimming speed and $\text{MO}_{2\text{cor}}$, regression analysis of exponential equations using a parametric analysis of variance (ANOVA) were used. A value of $P < 0.05$ was considered statistically significant.

**Results**

The statistical analysis by ANCOVA showed no significant parallelism of the
regression line for body length (P = 0.217 > 0.05) or body mass (P = 0.234 > 0.05) to compare the swimming abilities of chum and masu salmon in the laboratory. In the test of parallelism on regression line in the swimming performance (e.g. $U_{\text{crit}}$) in the laboratory study, $U_{\text{crit}}$ of male and female masu salmon was not significant (P = 0.895 > 0.05). Student’s t-test also revealed no significant differences (P > 0.05) in the swimming abilities in the laboratory or upstream-migration behavior in the field between females and males of chum and masu salmon.

Swimming abilities in the laboratory

The $U_{\text{crit}}$ values for the chum and masu salmon were 1.42 BL s$^{-1}$ and 1.89 BL s$^{-1}$, respectively, and masu salmon were significantly faster than chum salmon (P < 0.01; Fig. 3). The chum and masu salmon SMRs were 243.6 mgO$_2$h$^{-1}$ kg$^{-1}$ and 112.3 mgO$_2$h$^{-1}$ kg$^{-1}$, respectively, and the masu salmon’s SMR was significantly lower than that of chum salmon (P < 0.01; Fig. 3). The chum and masu salmon AMRs were 369.0 mgO$_2$h$^{-1}$ and 391.9 mgO$_2$h$^{-1}$ kg$^{-1}$, respectively. The chum and masu salmon AMSs were 174.1 mgO$_2$h$^{-1}$ kg$^{-1}$ and 272.8 mgO$_2$h$^{-1}$ kg$^{-1}$, respectively. The differences in AMR and AMS values between the 2 salmon species were not significant (Fig. 3).

During the swimming test, the rate of oxygen consumption (MO$_2$) tended to increase proportionally with swimming speed. No increases in MO$_2$ were observed at
low swimming speeds in masu salmon (Fig. 4A). Figure 4B shows the relationship
between the MO2cor and swimming speed on an exponentially curve. The exponential
curves satisfactorily fitted the data for chum and masu salmon, and a significant
difference was found between chum and masu salmon (P < 0.05). The COTnet was also
influenced by swimming speed. It is worth noting that the lowest COTnet was found at
0.5 and 1.0 BL s⁻¹, which were considered the optimal swimming speeds in chum
salmon and masu salmon, respectively (Fig. 5). Although the COTnet of masu salmon
tended to be lower than for chum salmon, there was no significant difference between
the two species (P > 0.05).

From the EMG data, the muscle-activity levels were significantly correlated with
swimming speed according to simple regression analysis for all chum and masu salmon
(average of 12 chum salmon in 2010 and 2011, r²=0.92, P<0.05; average of 9 masu
salmon in 2010 and 2011, r²=0.97, P<0.05). A simple regression analysis was used to
convert EMG signals to swimming speeds in the field study by avoiding EMG values
above 40 showing no change in swimming speed. In the plots of all fishes,
U=0.043EMG– 0.0138 for the chum salmon (Fig. 6A) and U=0.049EMG– 0.0487 for
the masu salmon (Fig. 6B), where U is swimming speed (BL s⁻¹) and EMG is the EMG
values.
Upstream-migration behavior in the field

In 2010 and 2011, EMG data for all chum and masu salmon were collected around the protection bed and groundsill #5. All tagged fish migrated upstream or downstream using the fish passages on the day of release, and none of the fish that entered fish passages at the protection bed and groundsill #5 made downstream migrations. Table 1 shows the percentage of passing fish. The passage rate for both chum and masu salmon at each structure dropped in 2011. At the fish passages of the ground sill #5, the passage rate for masu salmon did not change, but only one fish was observed passing successfully in 2011.

Figures 7 shows the water velocity and passage path at the fish passages of the protection bed and groundsill #5 in 2010 (A) and 2011 (B). In 2011, 60-80% of the fish passage area at the protection bed #5 was filled up by a sandbar because a severe typhoon hit Sapporo City in September 2011. As a result, the water velocity was greater in 2011 than in 2010. In 2010, all fish passed through the fish passages at the protection bed and groundsill #5, but the fish only passed along the sandbar at the protection bed #5.

Table 2 shows the swimming speed and approach time at the fish passages of the protection bed and groundsill #5 in 2010 and 2011. At the groundsill #5, chum and masu
salmon showed no difference in swimming speed and approach time in either 2010 or 2011.

Fig. 8 shows the time-course trajectory of swimming speeds of representative chum salmon (A, C) and masu salmon (B, D) through the fish passages. Non-aerobic swimming performance exceeding $U_{\text{crit}}$ was observed in both species at each step in the fish passages. In the pools of the fish passages, each fish swam relatively slowly, approaching the optimal swimming speed calculated in the laboratory. No significant difference was found the approaching time between chum and masu salmon at each step (P > 0.05).

The holding time at each step through the fish passage at the protection bed and groundsill #5 was significantly shorter for masu salmon than chum salmon in 2010 (P < 0.01; Fig. 9A), and the search time at each step through the fish passage at the protection bed and groundsill #5 was significantly longer for masu salmon than chum salmon in 2010 (P < 0.01) and 2011 (P < 0.05; Fig. 9B). There was also a significant difference in the search time for chum salmon between 2010 and 2011 (P < 0.01; Fig. 9B). Fig. 9C shows the number of trial times for each step through fish passage at the protection bed and groundsill #5. The number of trial times for the protection bed and groundsill #5 in 2010 was significantly shorter for masu salmon than chum salmon (P <
The number of times that fish were observed swimming at speeds greater than $U_{\text{crit}}$ at the protection bed and groundsill #5 was significantly lower for masu salmon than chum salmon in 2010 (Fig. 9D). In addition, the time over $U_{\text{crit}}$ for the protection bed and groundsill #5 was significantly longer for masu salmon than chum salmon in both 2010 and 2011 ($P < 0.01$; Fig. 9E).

**Discussion**

Swimming ability, measured using a swim tunnel in the laboratory, and upstream spawning-migration behavior, measured using EMG telemetry at the fish passages in the Toyohira River, were compared between chum and masu salmon. Masu salmon are better adapted to swimming in a high-water-velocity area for an extended periods of time than chum salmon, and this adaptability could make masu salmon more successful than chum salmon in completing a migration to their spawning ground in the upper reaches of the river.

Both the mean $\text{MO}_2$ throughout the swimming test and the $\text{COT}_{\text{net}}$ tended to be lower in masu salmon than chum salmon. This pattern was particularly obvious above 1 BL $s^{-1}$, where the $\text{COT}_{\text{net}}$ increased with speed in a parallel in the two species until 2 BL $s^{-1}$ (Fig. 5). Excess post-exercise oxygen consumption (EPOC) is estimated as the time
required to return to their normal level of oxygen consumption (recovery time) and the
total oxygen cost of swimming to $U_{\text{crit}}$ (Brett 1964; Lee et al. 2003b). Lee et al. (2003b)
and Farrell (2007) suggested that increase in the COT rate was estimated 20-50 % lower
than it was without EPOC. Although we did not examine EPOC in this study, the
COT_{net} increased in parallel with increasing the swimming speed over 1 BL^{-1} s in chum
and masu salmon.

Lee et al. (2003a) also showed that the MO_{2} routine, with properties similar to the
SMR, was no different between coho and sockeye salmon captured around the same
time. Both $U_{\text{crit}}$ and the optimal swimming speed were significantly faster for masu
salmon than chum salmon, and the SMR of masu salmon was significantly lower than
that of chum salmon in this study. Masu salmon spawning grounds are usually located
in the upper reaches of rivers (Kato 1991). Therefore, it is likely that masu salmon must
pass through more cross-river constructs with high-water-velocity than chum salmon. In
high-water-flow areas, masu salmon may swim use aerobic swimming more
successfully than chum salmon. As masu salmon stay in the river longer time than chum
salmon, the metabolic rate of masu salmon is lower than chum salmon. Therefore, it
was reasonable to assume that the basal metabolism of the masu salmon was lower than
chum salmon, and there was difference in slope of MO_{2,cor} between chum and masu
salmon. Lee et al. (2003a) showed that salmons, migrating for long-distance, the
attained a significantly higher $U_{\text{crit}}$ at and were more efficient swimmers at $U_{\text{crit}}$ because
of a lower $MO_{2\text{max}}$ compared with other salmons migrating for a comparatively short
distance. Masu salmon have higher $U_{\text{crit}}$ and lower SMR than chum salmon. However,
AMR was similar between chum and masu salmon in this study presumably because
that small sample sizes may have prevented detecting differences.

It is well known that water temperature influences the metabolism and swimming
performance of salmonids (Lee et al. 2003a; Farrell 2007). This study was carried out at
the water temperature of the Chitose River in autumn. It should be mentioned that a
significant change might be observed in the metabolism and swimming performance of
masu salmon at a higher water temperature (as in summer, before masu salmon start
their upstream migration). Lee et al. (2003a) investigated relationships between
swimming performance and metabolism for sockeye salmon of different stocks in the
swim test and found that fishes captured in the upper reaches of the river migrates much
longer distances and negotiate more severe hydraulic challenges than the coastal fish.
Compared to chum salmon, masu salmon have their spawning grounds farther upriver
and remain in the river longer time; therefore, masu salmon are better adapted to swim
for extended time in an area of high-water-velocity.
The MO$_2$ of both species tended to plateau before reaching $U_{\text{crit}}$ (Fig. 4A), and the slopes of the COT$_{\text{net}}$ shifted between 1.75 BL s$^{-1}$ and 2 BL s$^{-1}$ in both species (Fig. 5), the slopes of the EMG shifted between 1.5 BL s$^{-1}$ and 2 BL s$^{-1}$ in both species (Fig. 6). The amplitude and frequency of these pulses was directly correlated to the level of red-muscle activity (Beddow and McKinley 1999; Økland et al. 1997), indicating that the shift in muscle performance from white muscle to red muscle occurred between 1.5 BL s$^{-1}$ and 2 BL s$^{-1}$; this result suggests that supplementary swimming effort when approaching $U_{\text{crit}}$ was sustained by anaerobic metabolism. Farrell (2007) indicated that the oxygen requirements should either plateau or decrease at nearly $U_{\text{crit}}$ because of the activation of white muscle (based on electro-myography recordings) and glycolysis (based on glycogen depletion and lactate accumulation in white muscle); however, Farrell (2007) also explained that white-muscle contraction has a significant aerobic component that drives an increase in MO$_2$ near $U_{\text{crit}}$. White muscle has aerobic capacity and is activated at speeds below $U_{\text{crit}}$. Therefore, the metabolic cost of swimming increases exponentially with velocity (Fig. 4B).

In the field study, the searching time was significantly longer for masu salmon than chum salmon, and non-aerobic swimming performance exceeding $U_{\text{crit}}$ was necessary for both two species at each step in the fish passages because they had to swim at high
flow rate (exceeding 2m$^{-1}$ s). It is likely that masu salmon could search long periods of
time in the each pool in order to find easy routes for the reduction of energy loss.

Gowans et al. (1999) reported that migrating Atlantic salmon ($Salmo salar$) sometimes
failed to locate the entrance to a pool of fish passage and appeared to be attracted by
tailrace and turbine flows. Makiguchi et al. (2011) indicated that it was important for the
successful migration that salmon find passage upstream rapidly and easily without
wandering. Our results suggested that masu salmon search approach routes, reducing
energy expended in approaching the fish passages compared to chum salmon.

Hinch and Bratty (2000) tracked adult sockeye salmon during upstream migration
using EMG telemetry at Hell’s Gate in the Fraser River and reported that swimming
speed patterns alternated at different time scales between relatively fast and slow speeds.
In our study, the search time was significantly longer for masu salmon than chum
salmon, but the number of times over $U_{crit}$ at each fish passages were significantly lower
for masu salmon than chum salmon. Masu salmon could select slow and rapid
swimming, depending on the river obstacle, and chum and masu salmon searched for
routes of approach at speeds approximating the optimal swimming speed. Hinch and
Rand (2000) reported that successful sockeye salmons swan at the Hell’s Gate, and
migrated according to an optimal swimming speed model range in whole of Fraser
River, which migrants minimized transport costs per unit distance. Our study also showed that successful chum and masu salmon used the energy-saving swimming at fish passages. In fact the fish passages were organized by some steps to secure recovering time in the Toyohira River, successful chum and masu salmon could almost use optimal swimming speed except over the $U_{\text{crit}}$ swimming at each step.

Chum salmon, however, had longer holding times and shorter search times than masu salmon at each fish passage. Because the holding time occurred when each fish crossed to the next step in the fish passage, this finding indicated that the holding time occurred before or after the burst speed over $U_{\text{crit}}$. During upstream migration, chum salmon had a consistent holding behavior after swimming at high speed over $U_{\text{crit}}$, indicating that they swim at speeds greater than $U_{\text{crit}}$ prior to holding (Makiguchi et al., 2007). Chum salmon showed the more trial than masu salmon at each fish passage, indicating that chum salmon swim over $U_{\text{crit}}$.

Lee et al. (2003b) reported that routine oxygen consumption was restored within approximately 1 h in adult sockeye salmon in the EPOC test. In our study, if the holding time was defined as the recovery time after excess swimming, chum salmon spent approximately 15-20 minutes in recovery at each steps. These observations may show that chum salmon suffered an energy loss at the fish passages; extended periods of
swimming at fast speeds may deplete the limited energy reserves of fish and leave little
energy for additional upriver progress (Rand and Hinch 1998). It is also possible that
the sustained and repeated bouts of anaerobic activity (e.g., swimming at speeds over
\( U_{\text{crit}} \) for prolonged periods of time) could lead to mortality by causing lethal levels of
blood lactate to accumulate, resulting in metabolic acidosis (Hinch and Bratty, 2000). It
is possible that the loss of stored energy decreased the passing rate of chum salmon at
the ground sill #5 (see Table 2). Moreover, swimming over \( U_{\text{crit}} \) caused the fish fatigue
and stress. Webb (1971) reported that anaerobic metabolism occurred during swimming
at 80% of \( U_{\text{crit}} \). Chum salmon were considered more stressed than masu salmon because
the \( U_{\text{crit}} \) of chum salmon were lower than that of masu salmon.

In contrast, masu salmon required only approximately 10 minutes of recovery time,
suggesting two possibilities. First, masu salmon may be resilient to exceeding \( U_{\text{crit}} \).
Second, no more than 10 minutes was required to pass though the protection bed and
ground sill #5 in the Toyohira River. For example, the total length of the fish passage of
the protection bed and ground sill #5 was less than 50 m (8 pools; see Fig. 2), but the
vertical-slot fishway at the Seton River and the Fraser River, British Columbia, is more
than 100 m long (Hinch et al. 1996; Pon et al. 2009a). Nevertheless, more information is
needed regarding energy cost and metabolism (e.g., EPOC) and spawning behavior in
masu and chum salmon.

Percentages of fish passing the fish passage of the protection bed #5 were 67 % and 30 % in chum and masu salmon, respectively. It was unclear if the differences between successful and unsuccessful passages were due to swimming speed and approach time; however, it was likely that unsuccessful individuals gave up quickly at the fish passages or required a very long time to find passing routes. No significant difference was observed between 2010 and 2011 in migration behavior at each fish passage, except in the search time of chum salmon. The mean search time of masu salmon was lower in 2011 than 2010, when the routes had been filled up by a sandbar during the typhoon.

In conclusion, comparisons between chum salmon and masu salmon of both swimming ability in the laboratory swim tunnel and upstream-migration behavior using EMG telemetry at fish passages in the Toyohira River provided strong evidence that masu salmon were better adapted than chum salmon to swimming for an extended periods of time in areas of high-water-velocity. Masu salmon were better able to migrate upstream to their spawning grounds in the upper reaches of the river than chum salmon. In this study, swimming performance did not vary significantly with body length or mass; however, these differences should be analyzed by further morphological and genetic studies.
Acknowledgements

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References


Figure Captions

Figure 1. A map of the study site showing the experimental site in the Chitose Salmon Aquarium near the Chitose River (A), the positions of the groundsills, and chum and masu salmon release point in the Toyohira River (B).

Figure 2. A diagram of the fish passage of the protection bed #5 (a) and fish passage of the groundsill #5 (b). The dotted line represents the water’s edge for a typical water level in 2010. The number of circles in the fish passage is the pool number.

Figure 3. Average (± SE) standard metabolic rate (SMR), active metabolic rate (AMR), aerobic metabolic scope (AMS), and critical swimming speed ($U_{crit}$) for chum salmon (white column) and masu salmon (black column). The left Y axis corresponds to oxygen consumption (MO$_2$ in mgO$_2$ h$^{-1}$ kg$^{-1}$) related to SMR, AMR, and AMS. The right Y axis corresponds to swimming speed (BL $s^{-1}$) for $U_{crit}$. The asterisk indicates significant differences by Student’s t-test (P < 0.01).

Figure 4. (A) The relationship between the rate of oxygen consumption (MO$_2$) and swimming speed (BL $s^{-1}$) for chum salmon (solid line) and masu salmon (dotted line). (B) The relationship between the MO$_{2cor}$ and swimming speed (BL $s^{-1}$) for chum salmon (solid line) and masu salmon (dotted line). The relationship is exponential; for chum salmon, MO$_{2cor}$ = 224.39$e^{0.409U}$ (P < 0.05; $r^2$ = 0.952); for
masu salmon, \( \text{MO}_{2co} = 112.51 e^{0.734U} \) \((P < 0.05; r^2 = 0.903)\).

Figure 5. The relationships between net cost of transport \((\text{COT}_{\text{net}})\) and swimming speed \((\text{BL s}^{-1})\) for chum salmon (solid line) and masu salmon (dotted line). The \(\text{COT}_{\text{net}}\) varied for chum salmon according to the polynomial equation \(\text{COT}_{\text{net}} = 3.55 e^{-1} + 4.25 e^{-3} + 0.19 U^2 - U \) \((r^2=0.911)\) and for masu salmon according to the polynomial equation \(\text{COT}_{\text{net}} = 3.91 e^{-1} + 5.25 e^{-3} + 0.18 U^2 - U \) \((r^2=0.920)\).

Figure 6. The relationships between electromyogram (EMG) signals and swimming speed \((\text{BL s}^{-1})\) for chum salmon \((\text{A: n=12})\) and masu salmon \((\text{B: n=9})\) in all fish in the field study in 2010 and 2011. The standard error of each EMG value is expressed.

Figure 7. The swimming path (red dotted line) of passing chum and masu salmon and water velocity at the fish passage for the protection bed and groundsill #5 in 2010 \((\text{A})\) and 2011\((\text{B})\).

Figure 8. Time-series plots of swimming speeds of representative chum salmon in 2010\((\text{A})\) and 2011\((\text{C})\), and masu salmon in 2010 \((\text{B})\) and 2011\((\text{D})\). The dotted line represents the mean critical swimming speed \((U_{\text{crit}}; 1.42 \text{ BL}^{-1} \text{ s or 1.89 BL}^{-1} \text{ s})\) and optimal swimming speed \((U_{\text{opt}}; 0.5 \text{ BL}^{-1} \text{ s or 1.0 BL}^{-1} \text{ s})\) in chum salmon and masu salmon, respectively. The number of circles in the fish passage is the pool number.
in Fig. 2.

Figure 9. The holding time (A), searching time (B), number of trials (C), number of times over $U_{\text{crit}}$ (D) and over $U_{\text{crit}}$ time (E) at each fish passage step in the fish passage of the protection bed and groundsill #5 for chum salmon (white column) and masu salmon (black column) in 2010 and 2011. The asterisk indicates significant differences by Student’s t-test ($P < 0.01, 0.05$). The number of fish is provided in parentheses.
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<th>Releasing date</th>
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* Data in parentheses are the number of female fish
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* Values represent the mean ± standard error

** Data in parentheses are the number of female
Fig. 1

[Diagram of river systems and study sites with markers and labels]

Study site (B)

Ishikari River

Toyohira River

Chitose River

Release point

Study Site (A)

Chitose Salmon Aquarium

[Scale markers for km and (Km)]
Fig. 4

Swimming speed (BL s⁻¹)

MO₂ (mgO₂ h⁻¹ kg⁻¹)

MO₂cor (mgO₂ h⁻¹ kg⁻¹)
Fig. 5

\[ \text{COT}_{\text{net}} \text{ (mgO}_2\text{ h}^{-1}\text{ m}^{-1}) \]

- **Y-axis**: \[0 - 0.100\]
- **X-axis**: \[0 - 2\]

- **Line**: Continuous line
- **Dashed line**: Dashed line
- **Data points**: Diamond and square markers with error bars
Fig. 6

Graph A: Swimmer speed (BL s⁻¹) vs. EMG value

Graph B: Swimmer speed (BL s⁻¹) vs. EMG value
Fig. 8

Swimming Speed (BL s⁻¹)

A

19:30 19:50 20:10 20:30
2010/10/5

B

17:30 17:50 18:10 18:30
2010/9/26

C

18:00 18:10 18:20 18:30 18:40 18:50
2011/10/9

D

16:30 16:40 16:50 17:00
2011/9/28

U_{crit}  U_{opt}