Comparison of the swimming ability and upstream-migration behavior between chum salmon and masu salmon

Koji Miyoshi, Kazufumi Hayashida, Taku Sakashita, Makoto Fujii, Hisaya Nii, Katsuya Nakao, and Hiroshi Ueda

Koji Miyoshi, Kazufumi Hayashida, and Hiroshi Ueda. Division of Biosphere Science, Graduate School of Environmental Science, Hokkaido University, North 9 West 9, Kita-ku, Sapporo, Hokkaido 060-0809, Japan.

Kazufumi Hayashida. Watershed Environmental Engineering Research Team, Civil Engineering Research Institute for Cold Region, Hiragishi 1-3, Toyohira-ku, Sapporo, Hokkaido 062-8602, Japan.

Taku Sakashita, Makoto Fujii, Hisaya Nii, and Katsuya Nakao. Hokkaido Aquaculture Promotion Corporation, Yonesato 4-1-3-3, Shiroishi-ku, Sapporo, Hokkaido 003-0874, Japan.

Hiroshi Ueda. Field Science Center for Northern Biosphere, Hokkaido University, North 9 West 9, Kita-ku, Sapporo, Hokkaido 060-0809, Japan.

E-mail address of each author: K. Miyoshi: miyoshi0503@gmail.com, K. Hayashida: hayashida0109@gmail.com, T. Sakashita: sakashita@saibai.or.jp, M. Fujii: fujii@saibai.or.jp,

H. Nii: nii-h3181@saibai.or.jp, K. Nakao: nakao@saibai.or.jp, and H. Ueda: hueda@fsc.hokudai.ac.jp

Koji Miyoshi's present address. Abashiri Fisheries Research Institute, Fisheries Research Department, Hokkaido Research Organization, Masu Ura 1-1, Abashiri, Hokkaido 099-3119, Japan.

Corresponding author: Dr. Hiroshi Ueda, Field Science Center for Northern Biosphere, Hokkaido University, North 9 West 9, Kita-ku, Sapporo, Hokkaido 060-0809, Japan.
Tel and Fax number: +81-11-706-2598, e-mail address: hueda@fsc.hokudai.ac.jp

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

66 spawning migration of sockeye salmon in the Fraser River, British Columbia, Canada,
67 has been extensively examined (Hinch et al. 1996; Hinch and Rand 1998; Hinch and
68 Bratty 2000), and many physiological data have been reported: the average swimming
69 activity of sockeye salmon passing through Hell's Gate were higher than at any other
70 location in the Fraser Canyon and non-aerobic swimming performance exceeding
71 critical swimming speed (U_{crit}) had to be sustained over a long period of time. Roscoe
72 and Hinch (2010) reported that these barriers impede or hinder the spawning-migration
73 routes of salmon and result in reduced salmon populations. In response, a large number
74 of fish passages have been installed all over the world.

75 The recent rapid development of radio telemetry technology and methods make it
76 possible to observe the upstream-migration behavior of salmon (Cooke et al. 2004).
77 Fish telemetry with integrated muscle electromyogram (EMG) has been used to
78 examine the upstream migration of sockeye salmon (Hinch et al. 1996; Hinch & Bratty,
79 2000; Pon et al. 2009a, b). EMG can be used directly as an indicator of the intensity of
80 fish muscle activity and to evaluate the efficiency of fish passage in relation to the
81 swimming performance of Pacific salmon (Roscoe and Hinch 2010; Makiguchi et al.
82 2011).

83 In Hokkaido, Japan, the spawning seasons of chum salmon (*O. keta*) and masu

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

94 The purposes of this study were (1) to examine the relationship between swimming
95 speed and oxygen consumption, and compare swimming abilities of chum and masu
96 salmon in a swim tunnel in the laboratory using U_{crit}, standard metabolic rate (SMR),
97 active metabolic rate (AMR), and aerobic metabolic scope (AMS); (2) to investigate the
98 upstream-migration behaviors of chum and masu salmon in the field using EMG
99 telemetry to compare their behaviors at the fish passages in protection beds and
100 groundsills in the Toyohira River; and (3) to discuss their upstream spawning-migration
101 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

120 an acrylic board so that no gas exchange occurred, and water from the Chitose River
121 was pumped into it before the U_{crit} trial. The water temperature ranged from 12.0 to
122 13.5ºC and did not vary more than 1ºC during any experiments.
123 Fish were individually placed into the swimming chamber of the swim tunnel. In
124 all cases, fish were acclimated for 1 hour at 0.25 body lengths (BL) s^{-1} to minimize
125 handling effects before all U_{crit} trials. After each 15-min period, the water velocity was
126 increased by an additional 0.25 BL s^{-1} and was maintained at the new speed for 15 min
127 until the fish became fatigued or was unable to swim against the current. After the U_{crit}
128 trial was completed, body mass and fork length were measured. Flow-velocity values
129 were corrected to account for solid blocking effects (Gehrke et al. 1990), as described
130 by Bell and Terhune (1970).
131 The U_{crit} (BL s^{-1}) was calculated with Brett's formula (1964):
132 $$U_{crit} = U_i + (t \cdot t_i^{-1}) \cdot U \quad (1)$$
133 where U_i (BL s^{-1}) is the highest velocity maintained for the entire swimming period; t_i is
134 the prescribed swimming period (i.e., 15 min); t (min) is the amount of time spent at the
135 fatigue velocity; and U is the velocity increment (i.e., 0.25 BL s^{-1}).
136 To measure oxygen consumption (MO_2) during the acclimatization period and
137 during the U_{crit} trials, the oxygen concentration in the swim tunnel was measured

138 throughout the trial at 1-min intervals using a multi-water-quality sensor probe (U-50;
139 Horiba Ltd., Kyoto, Japan), which was housed inside the swim tunnel. Before the fish
140 were introduced, air bubbles were removed from the swim tunnel. Prior to each U_{crit}
141 trial, oxygen levels in the tunnel were reset by pumping fresh river water into the tunnel.
142 The MO_2 per 15-min period for each fish was calculated by subtracting the quantity of
143 oxygen at the end from the starting value. The MO_2 rate (mg O_2 kg-1 h-1) for individual
144 fish during a velocity increment was calculated as:
145 $MO_2 = [O_2]\ v/m$ (2)
146 where the rate of oxygen concentration $[O_2]$ is measured in mg O_2 per $l^{-1}\ h^{-1}$; v is the
147 water volume of the swim chamber (l); and m is the body mass of the fish (kg). MO_2
148 was then standardized to a value corrected for a fish of 1 kg (MO_{2cor}), using the
149 following allometric relationship derived by Schurmann and Steffensen (1997):
150 $$MO_{2cor} = MO_{2meas} \cdot (w \cdot w^{-1}_{cor})^{(1-A)} \quad (3)$$
151 where MO_{2meas} is the MO_2 measured during the trial; w is the mass of the fish; and w_{cor}
152 is the standard body mass of 1 kg. A is the condition factor [weight (g) /
153 length^3(cm)•100], calculated using the mean fork length and bodyweight for each
154 species.
155 Standard metabolic rate (SMR) is defined as the MO_2 at zero activity (Fry 1971;

156 Claireaux et al. 2006; Luna-Acosta et al. 2011). Because MO_2 was expected to increase
157 exponentially with swimming speed (Brett 1964), a curve was fitted for each individual,
158 according to the following equation:

159 $$MO_{2cor} = SMR \cdot \exp^{bU} \quad (4)$$

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

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

166 $$AMS = AMR–SMR \quad (5)$$

167 The net cost of transport (COT_{net}; mgO_2 kg^{-1} m^{-1}) was calculated as follows for
168 each swimming speed:

169 $$COT_{net} = MO_{2net} / U \quad (6)$$

170 where U is the swimming speed (m h^{-1}) and $MO_{2\text{-}net}$ is equal to the MO_2 at the
171 considered swimming speed minus SMR. AMR, SMR, AMS and COT_{net} values were
172 determined for each fish.

173

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

192 outdoor tanks at the Chitose Salmon Aquarium for calibration of the EMG signals to
193 swimming speeds. In 2010, 3 males (fork length, 56.4–74.1 cm; body weight 1.8–4.2
194 kg) and 3 females (fork length, 62.6–73.5 cm; body weight 2.7–3.9 kg) chum salmon,
195 and 3 males (fork length, 44.3–55.1 cm; body weight 0.9–1.8 kg) and 3 females (fork
196 length, 51.0–58.6 cm; body weight 1.5–2.5 kg) masu salmon were studied. In 2011, 1
197 male (fork length, 68.7 cm; body weight 3.3 kg) and 5 females (fork length, 54.6–69.5
198 cm; body weight 1.4–3.4 kg) chum salmon, and 2 males (fork length, 53.2–56.5 cm;
199 body weight 1.6–1.7 kg) and 1 female (fork length, 58.7 cm; body weight 2.6 kg) masu
200 salmon were studied.

201 Each fish was equipped with a cylindrical, epoxy-encased EMG transmitter
202 (CEMG-R11-35, Lotek Engineering Inc., Newmarket, Ontario, Canada; 18.3 g in air,
203 16.2 mm in diameter, and 53.0 mm in length) attached externally to the body surface
204 and positioned in front of the dorsal fin using the procedure developed by Makiguchi et
205 al. (2011). External attachment is suitable for short-term telemetry research, which
206 reduces handling stress for the fish (Bridger and Booth 2003; Makiguchi et al. 2007). To
207 attach the tag, experimental fish were anaesthetized using FA100 (eugenol; Tanabe
208 Seiyaku Co. Ltd, Osaka, Japan) at a concentration of 0.5 ml l^{-1} in water from the
209 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

228 to muscle activity was sampled at 2-s intervals. Individual samples were summed and
229 stored temporarily. At the end of the interval, the mean value was calculated, and an
230 activity level (EMG signal) ranging from 0 to 50 (no units) was assigned, and
231 transmitted to a radio receiver (model SRX_600; Lotek Engineering Inc.). The
232 attachment procedures usually required approximately 5 min to complete.

233 **Calibration of EMG signals to swimming speeds**

234 EMG signals were calibrated to swimming speed in the swim tunnel using
235 procedures developed by Makiguchi et al. (2011). The Chitose River water was poured
236 into the swim tunnel before each trial. The water temperature was set between 11.5 and
237 14.5ºC, which was similar to the water temperature at the capture point in the Toyohira
238 River. Experimental fish were individually placed into the swimming section of the
239 swim tunnel, and 10 EMG signals at 0 m s^{-1} were measured using the EMG radio
240 receiver when the fish maintained a holding position. Next, the trial was started at 0.3 m
241 s^{-1}, and the water velocity was increased incrementally by 0.3 m s^{-1}, with 10 EMG
242 signals measured at each increment. Fish readily swam against the current and rarely
243 came in contact with the grid at the back of the swim chamber. The trial ended at 1.2 m
244 s^{-1}. We used the average EMG output at each velocity for each fish to calibrate
245 transmitter output to swimming speed. We evaluated the relationship between the mean

246 EMG output and water velocity using a linear regression analysis.

247 **Field Study**

248 Few studies report that fish with EMG transmitters were calibrated in respirometers
249 prior to their release. In September and October of 2010 and 2011, chum and masu
250 salmon used in the EMG-calibration experiment were individually released in the study
251 area and tracked on foot during upstream migration using a hand-held directional Yagi
252 antenna (Table 1). The position of each individual was determined using
253 EMG-transmitter signals received by three SRX_600 radio receivers. The radio
254 receivers recorded EMG signals at 2-s intervals. Migration time in each segment was
255 measured for each fish by subtracting the time on reaching the exit from the time at
256 entry. The chum and masu salmon were often observed to have stopped swimming
257 during their upstream migration, and more than 3 min of swimming cessation during
258 upstream migration was defined as holding behavior. The calculation of swimming time
259 did not include holding time. EMG signals were converted to swimming speed using the
260 equations established from the EMG calibration for each fish. After tracking, water
261 depth was measured at 0.2-m intervals in the water column, and water velocity was
262 measured at 2–5-m intervals along the tracking area. All tagged fish were released
263 below protection bed #5, and the tagged fish were tracked intermittently for

approximately 2–5 days. The number of times the fish exceeded U_{crit} and the time spent swimming over U_{crit} were calculated from the time-course trajectory of swim speed, using the U_{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 MO_{2cor}, 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

282 regression line for body length ($P = 0.217 > 0.05$) or body mass ($P = 0.234 > 0.05$) to
283 compare the swimming abilities of chum and masu salmon in the laboratory. In the test
284 of parallelism on regression line in the swimming performance (e.g. U_{crit}) in the
285 laboratory study, U_{crit} of male and female masu salmon was not significant ($P = 0.895 >$
286 0.05). Student's t-test also revealed no significant differences ($P > 0.05$) in the
287 swimming abilities in the laboratory or upstream-migration behavior in the field
288 between females and males of chum and masu salmon.
289 **Swimming abilities in the laboratory**
290 The U_{crit} values for the chum and masu salmon were 1.42 BL s^{-1} and 1.89 BL s^{-1},
291 respectively, and masu salmon were significantly faster than chum salmon ($P < 0.01$;
292 Fig. 3). The chum and masu salmon SMRs were 243.6 mgO_2h^{-1} kg^{-1} and 112.3 mgO_2
293 h^{-1} kg^{-1}, respectively, and the masu salmon's SMR was significantly lower than that of
294 chum salmon ($P < 0.01$; Fig. 3). The chum and masu salmon AMRs were 369.0 mgO_2
295 h^{-1} kg^{-1} and 391.9 mgO_2 h^{-1} kg^{-1}, respectively. The chum and masu salmon AMSs were
296 174.1 mgO_2 h^{-1} kg^{-1} and 272.8 mgO_2 h^{-1} kg^{-1}, respectively. The differences in AMR
297 and AMS values between the 2 salmon species were not significant (Fig. 3).
298 During the swimming test, the rate of oxygen consumption (MO_2) tended to
299 increase proportionally with swimming speed. No increases in MO_2 were observed at

300 low swimming speeds in masu salmon (Fig. 4A). Figure 4B shows the relationship
301 between the MO_{2cor} and swimming speed on an exponentially curve. The exponential
302 curves satisfactorily fitted the data for chum and masu salmon, and a significant
303 difference was found between chum and masu salmon ($P < 0.05$). The COT_{net} was also
304 influenced by swimming speed. It is worth noting that the lowest COT_{net} was found at
305 0.5 and 1.0 BL s^{-1}, which were considered the optimal swimming speeds in chum
306 salmon and masu salmon, respectively (Fig. 5). Although the COT_{net} of masu salmon
307 tended to be lower than for chum salmon, there was no significant difference between
308 the two species ($P > 0.05$).

309 From the EMG data, the muscle-activity levels were significantly correlated with
310 swimming speed according to simple regression analysis for all chum and masu salmon
311 (average of 12 chum salmon in 2010 and 2011, r^2=0.92, P<0.05; average of 9 masu
312 salmon in 2010 and 2011, r^2=0.97, P<0.05). A simple regression analysis was used to
313 convert EMG signals to swimming speeds in the field study by avoiding EMG values
314 above 40 showing no change in swimming speed. In the plots of all fishes,
315 U=0.043*EMG*– 0.0138 for the chum salmon (Fig. 6A) and U=0.049*EMG*– 0.0487 for
316 the masu salmon (Fig. 6B), where U is swimming speed (BL s^{-1}) and EMG is the EMG
317 values.

318 **Upstream-migration behavior in the field**

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

327 Figures 7 shows the water velocity and passage path at the fish passages of the
328 protection bed and groundsill #5 in 2010 (A) and 2011 (B). In 2011, 60-80% of the fish
329 passage area at the protection bed #5was filled up by a sandbar because a severe
330 typhoon hit Sapporo City in September 2011. As a result, the water velocity was greater
331 in 2011 than in 2010. In 2010, all fish passed through the fish passages at the protection
332 bed and groundsill #5, but the fish only passed along the sandbar at the protection bed
333 #5.

334 Table 2 shows the swimming speed and approach time at the fish passages of the
335 protection bed and groundsill #5 in 2010 and 2011. At the groundsill #5, chum and masu

336 salmon showed no difference in swimming speed and approach time in either 2010 or
337 2011.

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

345 The holding time at each step through the fish passage at the protection bed and
346 groundsill #5 was significantly shorter for masu salmon than chum salmon in 2010 ($P <$
347 0.01; Fig. 9A), and the search time at each step through the fish passage at the
348 protection bed and groundsill #5 was significantly longer for masu salmon than chum
349 salmon in 2010 ($P < 0.01$) and 2011 ($P < 0.05$; Fig. 9B). There was also a significant
350 difference in the search time for chum salmon between 2010 and 2011 ($P < 0.01$; Fig.
351 9B). Fig. 9C shows the number of trial times for each step through fish passage at the
352 protection bed and groundsill #5. The number of trial times for the protection bed and
353 groundsill #5 in 2010 was significantly shorter for masu salmon than chum salmon ($P <$

354 0.01). The number of times that fish were observed swimming at speeds greater than
355 U_{crit} at the protection bed and groundsill #5 was significantly lower for masu salmon
356 than chum salmon in 2010 (Fig. 9D). In addition, the time over U_{crit} for the protection
357 bed and groundsill #5 was significantly longer for masu salmon than chum salmon in
358 both 2010 and 2011 ($P < 0.01$; Fig. 9E).
359

360 ## Discussion

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

368 Both the mean MO_2 throughout the swimming test and the COT_{net} tended to be
369 lower in masu salmon than chum salmon. This pattern was particularly obvious above 1
370 BL s^{-1}, where the COT_{net} increased with speed in a parallel in the two species until 2 BL
371 s^{-1} (Fig. 5). Excess post-exercise oxygen consumption (EPOC) is estimated as the time

372 required to return to their normal level of oxygen consumption (recovery time) and the
373 total oxygen cost of swimming to U_{crit} (Brett 1964; Lee et al. 2003b). Lee et al. (2003b)
374 and Farrell (2007) suggested that increase in the COT rate was estimated 20-50 % lower
375 than it was without EPOC. Although we did not examine EPOC in this study, the
376 COT_{net} increased in parallel with increasing the swimming speed over 1 BL^{-1} s in chum
377 and masu salmon.

378 Lee et al. (2003a) also showed that the MO_2 routine, with properties similar to the
379 SMR, was no different between coho and sockeye salmon captured around the same
380 time. Both U_{crit} and the optimal swimming speed were significantly faster for masu
381 salmon than chum salmon, and the SMR of masu salmon was significantly lower than
382 that of chum salmon in this study. Masu salmon spawning grounds are usually located
383 in the upper reaches of rivers (Kato 1991). Therefore, it is likely that masu salmon must
384 pass through more cross-river constructs with high-water-velocity than chum salmon. In
385 high-water-flow areas, masu salmon may swim use aerobic swimming more
386 successfully than chum salmon. As masu salmon stay in the river longer time than chum
387 salmon, the metabolic rate of masu salmon is lower than chum salmon. Therefore, it
388 was reasonable to assume that the basal metabolism of the masu salmon was lower than
389 chum salmon, and there was difference in slope of $MO2_{cor}$ between chum and masu

390 salmon. Lee et al. (2003a) showed that salmons, migrating for long-distance, the
391 attained a significantly higher U_{crit} at and were more efficient swimmers at U_{crit} because
392 of a lower MO_{2max} compared with other salmons migrating for a comparatively short
393 distance. Masu salmon have higher U_{crit} and lower SMR than chum salmon. However,
394 AMR was similar between chum and masu salmon in this study presumably because
395 that small sample sizes may have prevented detecting differences.
396 It is well known that water temperature influences the metabolism and swimming
397 performance of salmonids (Lee et al. 2003a; Farrell 2007). This study was carried out at
398 the water temperature of the Chitose River in autumn. It should be mentioned that a
399 significant change might be observed in the metabolism and swimming performance of
400 masu salmon at a higher water temperature (as in summer, before masu salmon start
401 their upstream migration). Lee et al. (2003a) investigated relationships between
402 swimming performance and metabolism for sockeye salmon of different stocks in the
403 swim test and found that fishes captured in the upper reaches of the river migrates much
404 longer distances and negotiate more severe hydraulic challenges than the coastal fish.
405 Compared to chum salmon, masu salmon have their spawning grounds farther upriver
406 and remain in the river longer time; therefore, masu salmon are better adapted to swim
407 for extended time in an area of high-water-velocity.

408 The MO_2 of both species tended to plateau before reaching U_{crit} (Fig.4A), and the
409 slopes of the COT_{net} shifted between 1.75 BL s^{-1} and 2 BL s^{-1} in both species (Fig.5), the
410 slopes of the EMG shifted between 1.5 BL s^{-1} and 2 BL s^{-1} in both species (Fig. 6). The
411 amplitude and frequency of these pulses was directly correlated to the level of
412 red-muscle activity (Beddow and McKinley 1999; Økland et al. 1997), indicating that
413 the shift in muscle performance from white muscle to red muscle occurred between 1.5
414 BL s^{-1} and 2 BL s^{-1}; this result suggests that supplementary swimming effort when
415 approaching U_{crit} was sustained by anaerobic metabolism. Farrell (2007) indicated that
416 the oxygen requirements should either plateau or decrease at nearly U_{crit} because of the
417 activation of white muscle (based on electro-myography recordings) and glycolysis
418 (based on glycogen depletion and lactate accumulation in white muscle); however,
419 Farrell (2007) also explained that white-muscle contraction has a significant aerobic
420 component that drives an increase in MO_2 near U_{crit}. White muscle has aerobic capacity
421 and is activated at speeds below U_{crit}. Therefore, the metabolic cost of swimming
422 increases exponentially with velocity (Fig. 4B).
423 In the field study, the searching time was significantly longer for masu salmon than
424 chum salmon, and non-aerobic swimming performance exceeding U_{crit} was necessary
425 for both two species at each step in the fish passages because they had to swim at high

426 flow rate (exceeding $2m^{-1}$ s). It is likely that masu salmon could search long periods of
427 time in the each pool in order to find easy routes for the reduction of energy loss.
428 Gowans et al. (1999) reported that migrating Atlantic salmon (*Salmo salar*) sometimes
429 failed to locate the entrance to a pool of fish passage and appeared to be attracted by
430 tailrace and turbine flows. Makiguchi et al. (2011) indicated that it was important for the
431 successful migration that salmon find passage upstream rapidly and easily without
432 wandering. Our results suggested that masu salmon search approach routes, reducing
433 energy expended in approaching the fish passages compared to chum salmon.
434 Hinch and Bratty (2000) tracked adult sockeye salmon during upstream migration
435 using EMG telemetry at Hell's Gate in the Fraser River and reported that swimming
436 speed patterns alternated at different time scales between relatively fast and slow speeds.
437 In our study, the search time was significantly longer for masu salmon than chum
438 salmon, but the number of times over U_{crit} at each fish passages were significantly lower
439 for masu salmon than chum salmon. Masu salmon could select slow and rapid
440 swimming, depending on the river obstacle, and chum and masu salmon searched for
441 routes of approach at speeds approximating the optimal swimming speed. Hinch and
442 Rand (2000) reported that successful sockeye salmons swan at the Hell's Gate, and
443 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_{cirt} 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_{crit}. During upstream migration, chum salmon had a consistent holding behavior after swimming at high speed over U_{crit}, indicating that they swim at speeds greater than U_{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_{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

462 swimming at fast speeds may deplete the limited energy reserves of fish and leave little
463 energy for additional upriver progress (Rand and Hinch 1998). It is also possible that
464 the sustained and repeated bouts of anaerobic activity (e.g., swimming at speeds over
465 U_{crit} for prolonged periods of time) could lead to mortality by causing lethal levels of
466 blood lactate to accumulate, resulting in metabolic acidosis (Hinch and Bratty, 2000). It
467 is possible that the loss of stored energy decreased the passing rate of chum salmon at
468 the groundsill #5 (see Table 2). Moreover, swimming over U_{crit} caused the fish fatigue
469 and stress. Webb (1971) reported that anaerobic metabolism occurred during swimming
470 at 80% of U_{crit}. Chum salmon were considered more stressed than masu salmon because
471 the U_{crit} of chum salmon were lower than that of masu salmon.
472 In contrast, masu salmon required only approximately 10 minutes of recovery time,
473 suggesting two possibilities. First, masu salmon may be resilient to exceeding U_{crit}.
474 Second, no more than 10 minutes was required to pass though the protection bed and
475 groundsill #5 in the Toyohira River. For example, the total length of the fish passage of
476 the protection bed and groundsill #5 was less than 50 m (8 pools; see Fig. 2), but the
477 vertical-slot fishway at the Seton River and the Fraser River, British Columbia, is more
478 than100 m long (Hinch et al. 1996; Pon et al. 2009a). Nevertheless, more information is
479 needed regarding energy cost and metabolism (e.g., EPOC) and spawning behavior in

480 masu and chum salmon.

481 Percentages of fish passing the fish passage of the protection bed #5 were 67 % and
482 30 % in chum and masu salmon, respectively. It was unclear if the differences between
483 successful and unsuccessful passages were due to swimming speed and approach time;
484 however, it was likely that unsuccessful individuals gave up quickly at the fish passages
485 or required a very long time to find passing routes. No significant difference was
486 observed between 2010 and 2011 in migration behavior at each fish passage, except in
487 the search time of chum salmon. The mean search time of masu salmon was lower in
488 2011 than 2010, when the routes had been filled up by a sandbar during the typhoon.

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

Acknowledgements

We thank the following people and organizations for their help and cooperation: Mr. M. Kikuchi of the Chitose Salmon Aquarium for the use of the Chitose Salmon Aquarium facilities, the staffs of the Sapporo Salmon Museum for valuable information about the Toyohira River, and the Sapporo River Office, Hokkaido Regional Development Bureau for valuable input on the selection of the experimental site.

References

Beddow, T.A., and McKinley, R.S. 1999. Importance of electrode positioning in biotelemetry studies estimating muscle activity in fish. J. Fish Biol. 54(4): 819-831. doi: 10.1111/j.1095-8649.1999.tb02035.x

Bell, W.M. and Terhune, L.D.B. 1970. Water tunnel design for fisheries research. Tech. Rep. Fish. Res. Bd Can. 195: 1-69.

Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Bd Can. 21(5): 1183-1226. doi: 10.1139/f64-103

Bridger, C.J., and Booth, R.K. 2003. The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. Rev. Fish. Sci. 11(1):

516 13-34.

517 Claireaux, G., Couturier, C., and Groison, A.L. 2006. Effect of temperature on

518 maximum swimming speed and cost of transport in juvenile European sea bass

519 (*Dicentrarchus labrax*). J. Exp. Biol. 209(17): 3420-3428. doi: 10.1242/jeb.0246.

520 Farrell, A.P. 2007. Cardiorespiratory performance during prolonged swimming tests

521 with salmonids: a perspective on temperature effects and potential analytical pitfalls.

522 Phil. Trans. R. So. B. 362(1487): 2017-2030. doi: 10.1098/rstb.2007.2111.

523 Fry, F. E. J. (1971). The effect of environmental factors on the physiology of fish. *In*

524 Fish Physiology. *Edited by* W.S. Hoar, and D. J. Randall. Academic Press, New

525 York, NY. pp. 1-98.

526 Gamperl, A. K., Rodnick, K. J., Faust, H. A., Venn, E. C., Byington, J. D., Bennett, M.

527 T., Crawshaw, L. I., Kelley, E. R., Powell, M. S. and Li, H. 2002. Metabolism,

528 swimming performance and tissue biochemistry of high desert redband trout

529 (*Oncorhynchus mykiss* ssp.): Evidence of phenotypic differences in physiological

530 function. Physiol. Biochem. Zool. 75(5): 413-431.

531 Gehrke, P.C., Fidler, L.E., Mense, D.C., and Randall, D.J. 1990. A respirometer with

532 controlled water-quality and computerized data acquisition for experiments with

533 swimming fish. Fish Physiol. Biochem. 8(1): 61-67. doi: 10.1007/BF00004432.

534 Gowans, A. R. D., J. D Armstrong and I. G. Priede, 1999. Movements of adult Atlantic
535 salmon in relation to a hydroelectric dam and fish ladder. J Fish Biol. 54(6):
536 713–726. doi: 10.1111/j.1095-8649.1999.tb02028.x
537 Hinch, S.G., Diewert, R.E., Lissimore, T.J., Prince, A.M.J., Healey, M.C., and
538 Henderson, M.A. 1996. Use of electromyogram telemetry to assess difficult
539 passage areas for river-migrating adult sockeye salmon. Trans. Am. Fish. Soc.
540 125(2): 253-260. doi: 10.1577/1548-8659(1996)125<0253:UOETTA>2.3.CO;2.
541 Hinch, S.G., and Bratty, J. 2000. Effects of swim speed and activity pattern on success
542 of adult sockeye salmon migration through an area of difficult passage. Trans. Am.
543 Fish. Soc. 129(2): 598-606. doi:
544 10.1577/1548-8659(2000)129<0598:EOSSAA>2.0.CO;2.
545 Hinch, S.G., and Rand, P.S. 2000. Optimal swimming speeds and forward-assisted
546 propulsion: energy-conserving behaviours of upriver-migrating adult salmon. Can.
547 J. Fish. Aquat. Sci. 57: 2470–2478. doi: 10.1139/f00-238.
548 Kato, F. 1991. Life history of masu and amago salmon (*Oncorhynchus masou* and
549 *Oncorhynchus rhodurus*). *In* Pacific Salmon Life Histories. *Edited by* C. Groot and
550 L. Margolis. University of British Columbia Press, Vancouver, B.C. pp. 427-520.
551 Lee, C.G., Farrell, A.P., Lotto, A., MacNutt, M.J., Hinch, S.G., and Healey, M.C. 2003a.

552 The effect of temperature on swimming performance and oxygen consumption in
553 adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. J. Exp.
554 Biol. 206(18): 3239-3251. doi: 10.1242/jeb.00547.
555 Lee, C.G., Farrell, A.P., Lotto, A., Hinch, S.G., and Healey, M.C. 2003b. Excess
556 post-exercise oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and
557 coho (*O. kisutch*) salmon following critical speed swimming. J. Exp. Biol. 206(18):
558 3253-3260. doi: 10.1242/jeb.00548.
559 Luna-Acosta, A., Lefrançois, C., Millot, S., Chatain, B., and Bégout, M.L. 2011.
560 Physiological response in different strains of sea bass (*Dicentrarchus labrax*):
561 Swimming and aerobic metabolic capacities. Aquaculture 317(1-4): 162-167.
562 doi:10.1016/j.aquaculture.2011.03.004.
563 Makiguchi, Y., Nii, H., Nakao, K., and Ueda, H. 2007. Upstream migration of adult
564 chum and pink salmon in the Shibetsu River. Hydrobiologia 582: 43-54. doi:
565 10.1007/s10750-006-0555-8.
566 Makiguchi, Y., Konno, Y., Konishi, K., Miyoshi, K., Sakashita, T., Nii, H., Nakao, K.,
567 and Ueda, H. 2011. EMG telemetry studies on upstream migration of chum salmon
568 in the Toyohira River, Hokkaido, Japan. Fish Physiol. Biochem. 37(2): 273-284.
569 doi: 10.1007/s10695-011-9495-y.

570 Mayama, H. 1992.Studies on the freshwater life and propagation technology of masu
571 salmon, *Oncorhynchus masou* (Brevoort). Sci. Rep. Hokkaido Salmon Hatch. 46:
572 1-156 (in Japanese with English summary).
573 Økland, F., Finstad, B., McKinley, R.S., Thorstad, E.B., and Booth, R.K. 1997.
574 Radio-transmitted electromyogram signals as indicators of physical activity in
575 Atlantic salmon. J. Fish Biol. 51(3): 476-488. doi:
576 10.1111/j.1095-8649.1997.tb01505.x.
577 Pon, L. B., Cooke, S. J. and Hinch, S. G. 2006. Passage efficiency and migration
578 behaviour of salmonid fishes at the Seton Dam fish passage. *Final report for the*
579 *Bridge Coastal Restoration Program*. Project 05.Se.01.
580 Pon, L.B., Hinch, S.G., Cooke, S.J., Patterson, D.A., and Farrell, A.P. 2009a. A
581 Comparison of the physiological condition, and fish passage time and success of
582 migrant adult sockeye salmon at Seton River Dam, British Columbia, under three
583 operational water discharge rates. N. Am. J. Fish. Manage. 29(5): 1195-1205. doi:
584 10.1577/M08-114.1.
585 Pon, L.B., Hinch, S.G., Cooke, S.J., Patterson, D.A., and Farrell, A.P. 2009b.
586 Physiological, energetic and behavioural correlates of successful fish passage of
587 adult sockeye salmon *Oncorhynchus nerka* in the Seton River, British Columbia. J

588 Fish Biol. 74(6): 1323-1336. doi: 10.1111/j.1095-8649.2009.02213.x.

589 Rand, P. S., and S. G. Hinch. 1998. Swim speeds and energy use of up-river migrating

590 sockeye salmon: simulating metabolic power and assessing risk of energy depletion.

591 Can. J. Fish. Aquat. Sci 55(8): 1832–1841. doi: 10.1139/f98-068

592 Roscoe, D.W., and Hinch, S.G. 2010. Effectiveness monitoring of fish passage facilities:

593 historical trends, geographic patterns and future directions. Fish Fish. 11(1): 12-33.

594 doi: 10.1111/j.1467-2979.2009.00333.x.

595 Salo, E. O. (1991). Life history of chum salmon (*Oncorhynchus ket*a). *In* Pacific Salmon

596 Life Histories. *Edited by* C. Groot and L. Margolis. University of British Columbia

597 Press, Vancouver, B.C. pp. 231-309.

598 Schurmann, H., and Steffensen, J.F. 1997. Effects of temperature, hypoxia and activity

599 on the metabolism of juvenile Atlantic cod. J. Fish Biol. 50(6): 1166-1180. doi:

600 10.1111/j.1095-8649.1997.tb01645.x.

601 Webb, P.W. 1971. Swimming Energetics of Trout .2. Oxygen Consumption and

602 Swimming Efficiency. J. Exp. Biol. 55(2): 521-540.

603 Wagner, G. N., Kuchel, L. J., Lotto, A., Patterson, D. A., Shrimpton, M., Hinch, S. G.,

604 and Farrell, A. P. 2006. Routine and Active Metabolic Rates of Migrating Adult

605 Wild Sockeye Salmon (*Oncorhynchus nerka* Walbaum) in Seawater and Freshwater.

606 Physiol. Biochem. Zool. 79(1): 100-108.

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, $MO_{2cor} = 224.39^{e0.409U}$ ($P < 0.05$; $r^2 = 0.952$); for

masu salmon, $MO_{2cor} = 112.51^{e0.734U}$ ($P < 0.05$; $r^2 = 0.903$).

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

Figure 6. The relationships between electromyogram (EMG) signals and swimming speed (BL s^{-1}) for chum salmon (A: n=12) and masu salmon (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 (A) and 2011(B).

Figure 8. Time-series plots of swimming speeds of representative chum salmon in 2010(A) and 2011(C), and masu salmon in 2010 (B) and 2011(D). The dotted line represents the mean critical swimming speed (U_{crit}; 1.42 BL^{-1} s or 1.89 BL^{-1} s) and optimal swimming speed (U_{opt}; 0.5 BL^{-1} s or 1.0 BL^{-1} 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_{crit} (D) and over U_{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.

Table. 1

Year	Species	Releasing point	Releasing date	Number of experimental fish (female)	Number of upstream migrating fish (female)		Number of passing fish (female)		Percentage of passing fish at the fishway	
					#5 protection bed	#5 ground sill	#5 protection bed	#5 ground sill	#5 protection bed	#5 ground sill
2010	chum	#5 protection bed	2010/10/6	6(3)	4(2)	4(2)	4(2)	2(2)	100	50
	masu		2010/9/26	6(3)	6(3)	6(3)	6(3)	6(3)	100	100
2011	chum		2011/10/4	6(5)	6(5)	4(3)	4(3)	1	67	25
	masu		2011/9/25	3(1)	3(1)	1	1	1	33	100

* Data in parentheses are the number of female fish

Table. 2

Year	Species	Swimming speed (BL/s)*		Approaching time (min)*	
		#5 Protection bed	#5 ground sill	#5 Protection bed	#5 ground sill
2010	chum	0.87 ± 7.3 (4)	1.33 (2)	38.2 ± 28.0 (4)	45.1 (2)
	masu	1.13 ± 6.6 (6)	1.28 ± 6.5 (6)	25.3 ± 19.2 (6)	58.9 ±37.1 (6)
2011	chum	1.14 ± 2.6 (4)	1.34 (1)	25.3 ± 16.5 (4)	16.5 (1)
	masu	1.38 ± 4.3 (3)	1.24 (1)	37.2 ± 4.3 (3)	16.0 (1)

* Values represent the mean ± standard error
** Data in parentheses are the number of female

Fig. 1

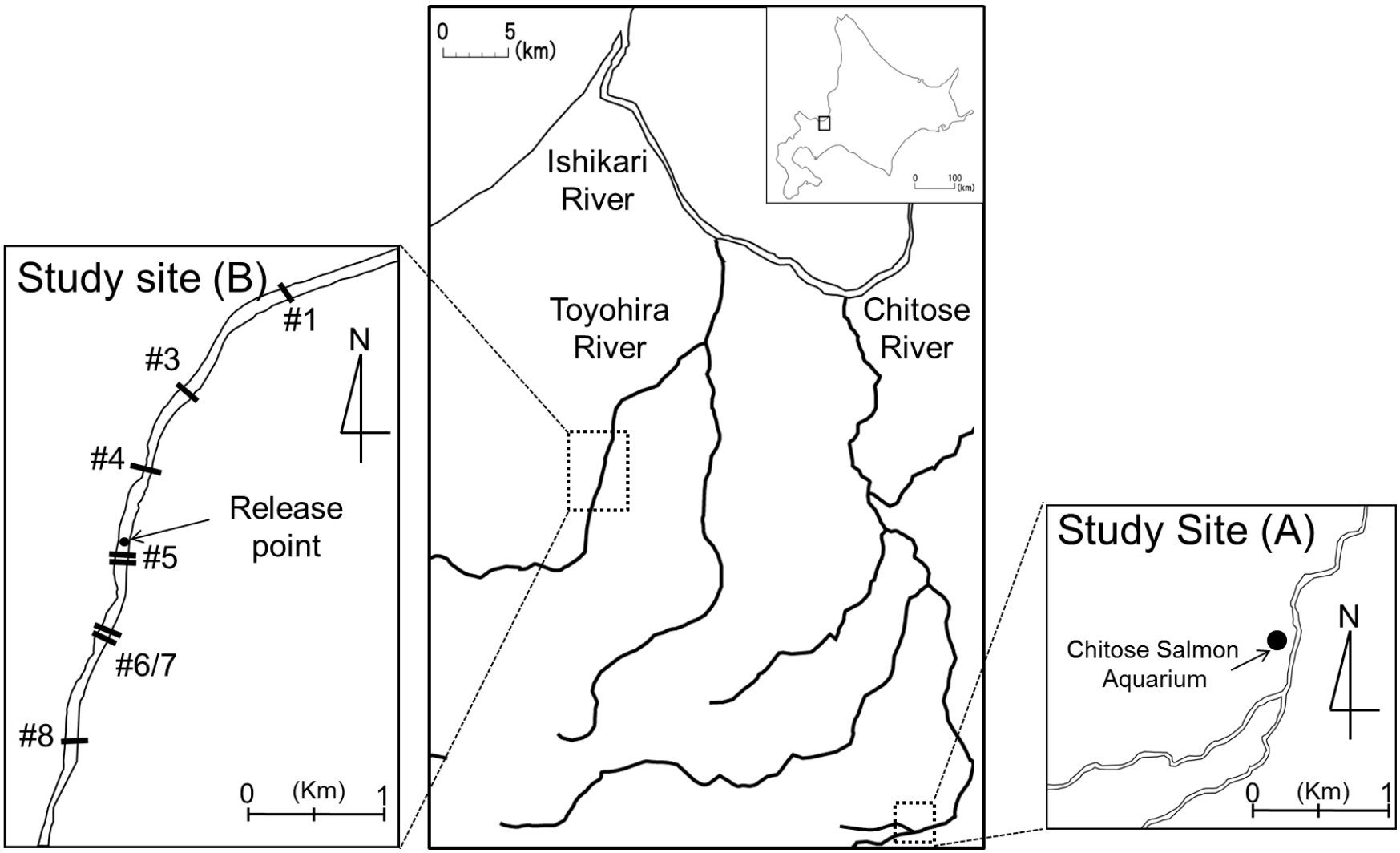

0 5 (km)
Ishikari River
Toyohira River
Chitose River
0 100 (km)
Study site (B)
#1
#3
#4
#5
#6/7
#8
N
Release point
0 (Km) 1
Study Site (A)
Chitose Salmon Aquarium
N
0 (Km) 1

Fig. 2

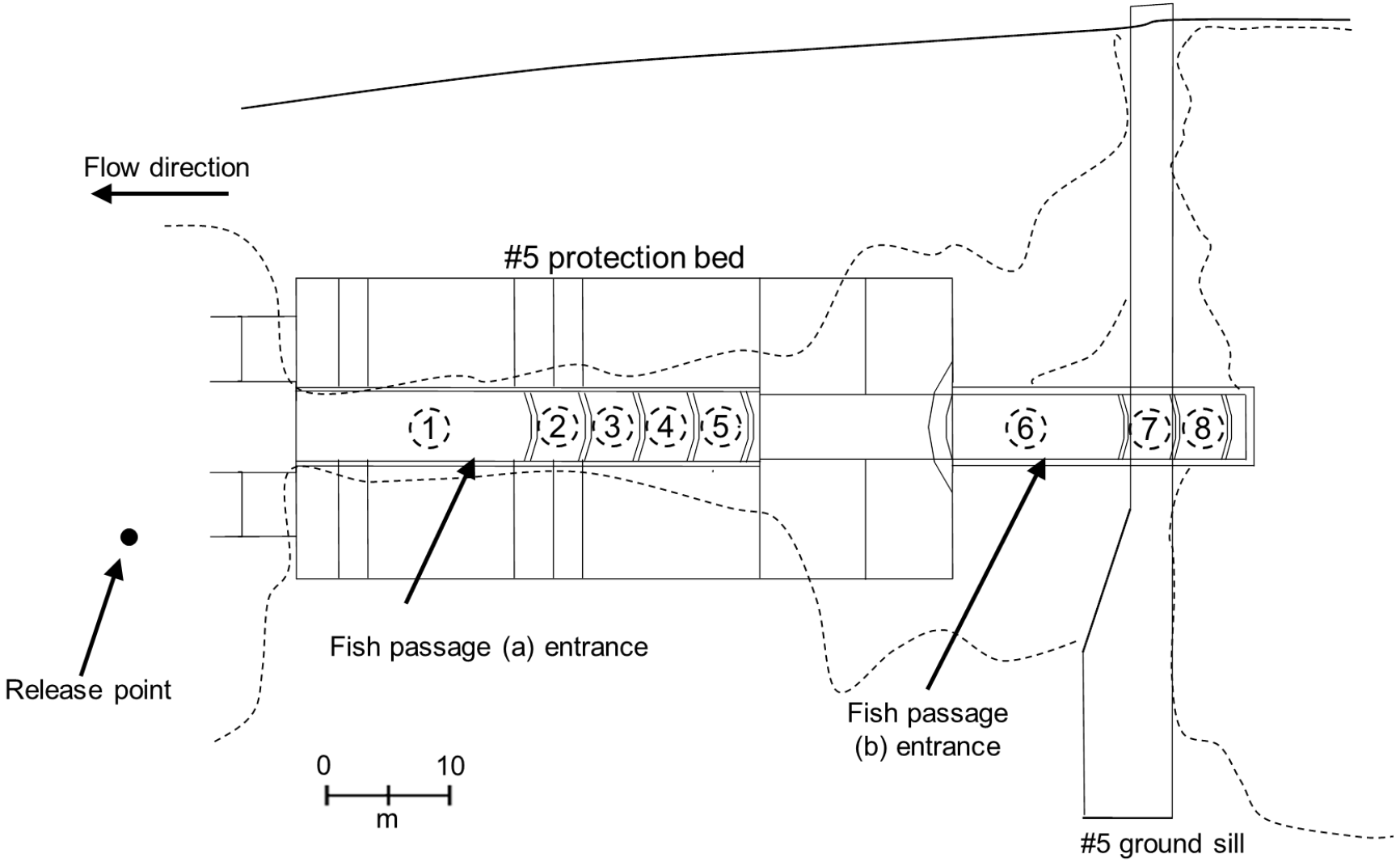

Flow direction
#5 protection bed
1
2
3
4
5
6
7
8
Release point
Fish passage (a) entrance
Fish passage
(b) entrance
0
10
m
#5 ground sill

Fig. 3

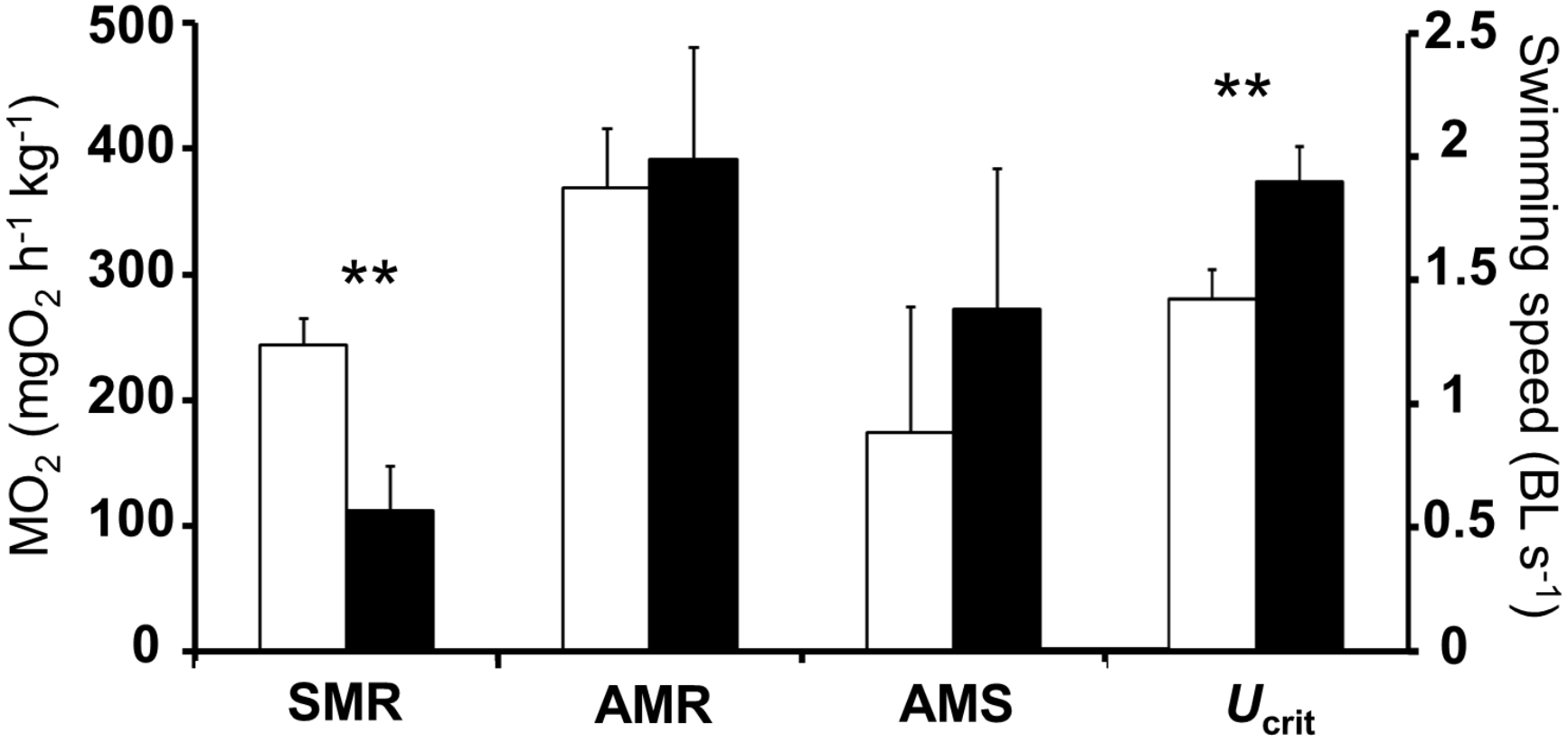
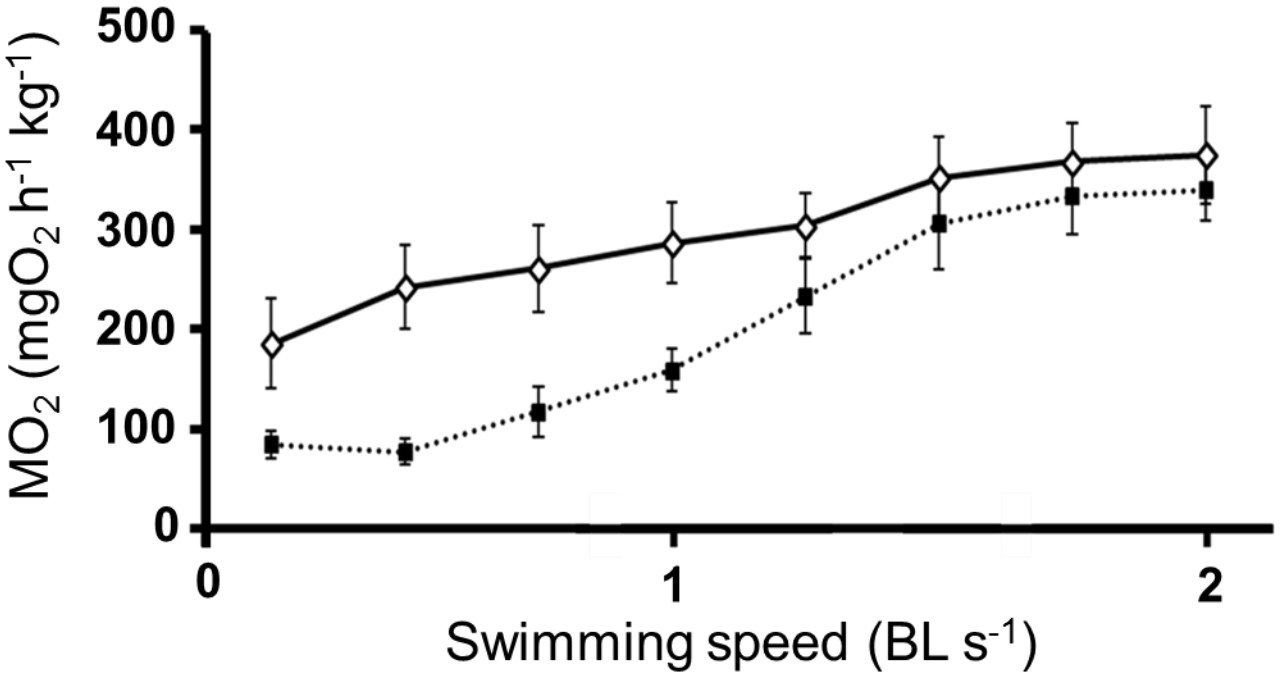

500
400
300
200
100
0
MO_2 (mgO_2 h^{-1} kg^{-1})
2.5
2
1.5
1
0.5
0
Swimming speed (BL s^{-1})
**
**
SMR
AMR
AMS
U_{crit}

Fig. 4


500
400
300
200
100
0
MO_2 (mgO_2 h^{-1} kg^{-1})
0
1
2
Swimming speed (BL s^{-1})

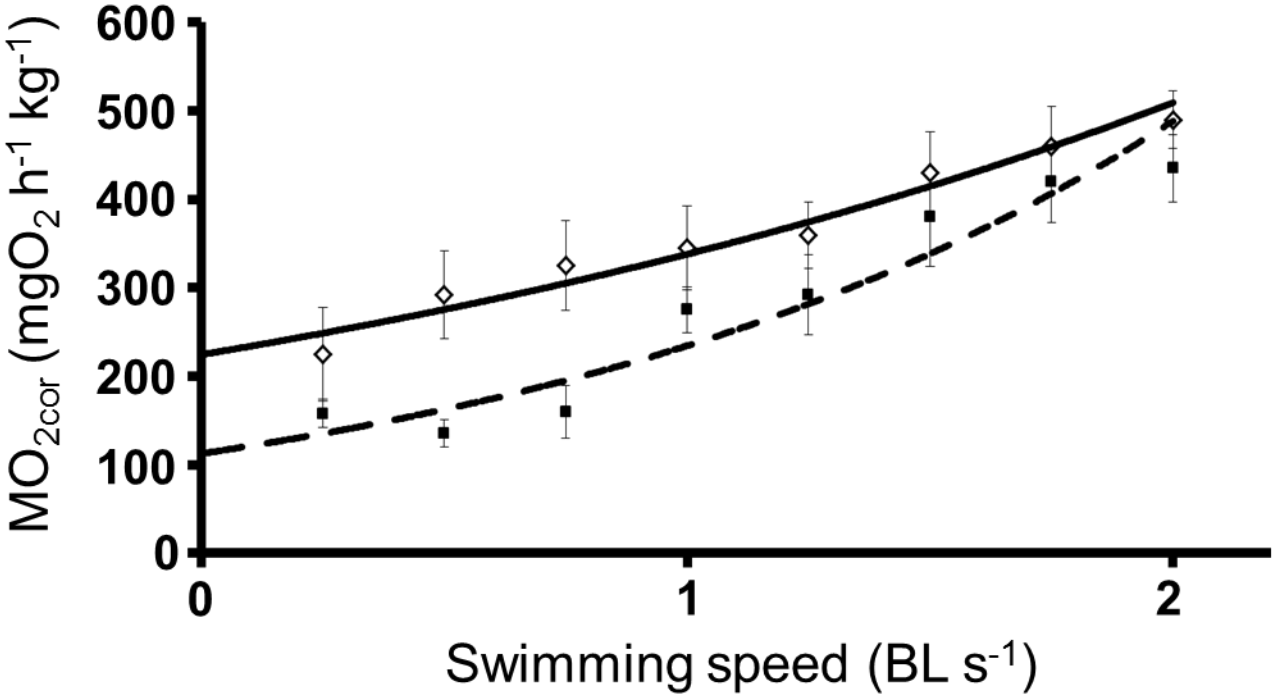

600
500
400
300
200
100
0
MO_{2cor} (mgO_2 h^{-1} kg^{-1})
0
1
2
Swimming speed (BL s^{-1})

Fig. 5

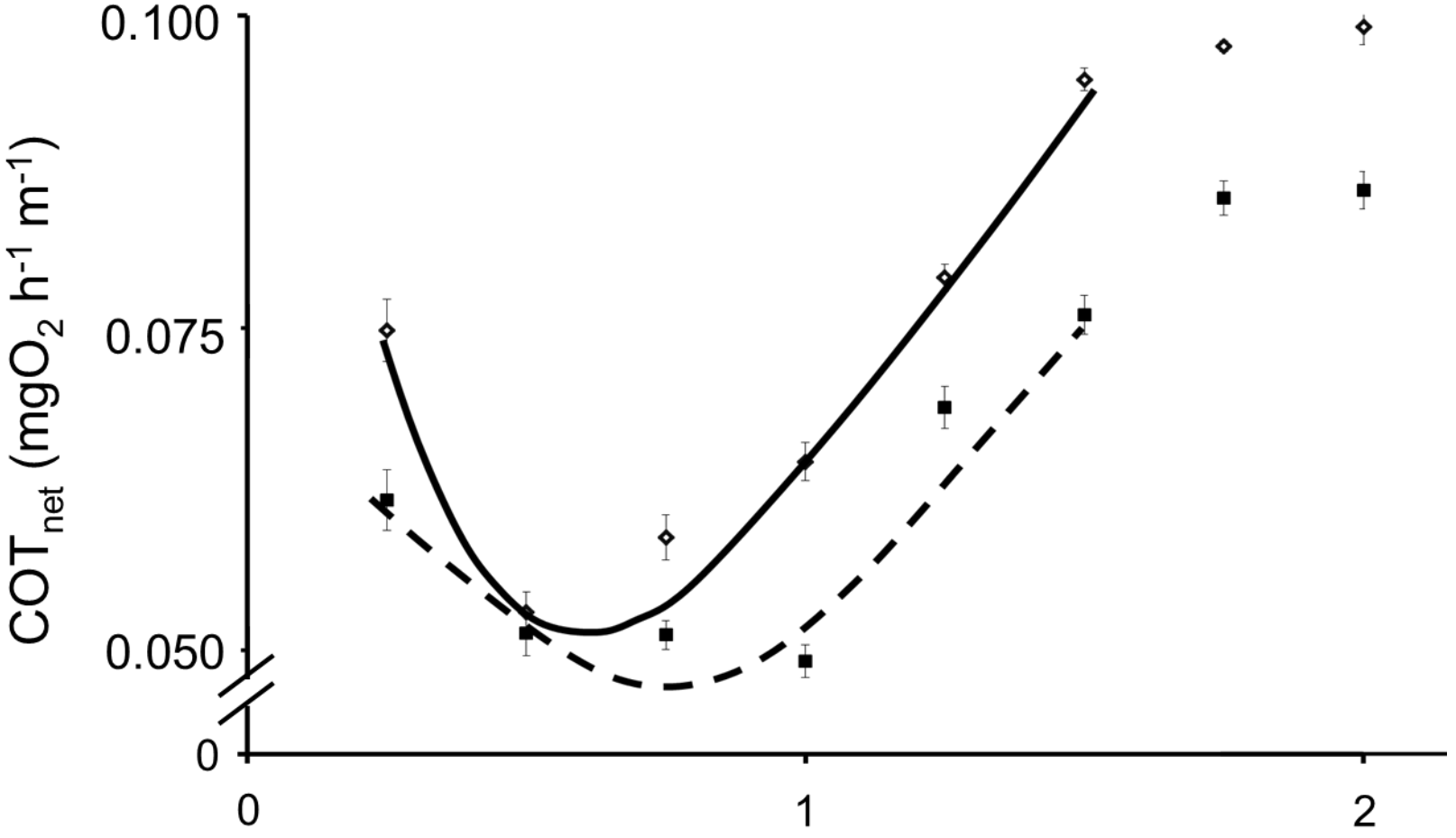


Fig. 6

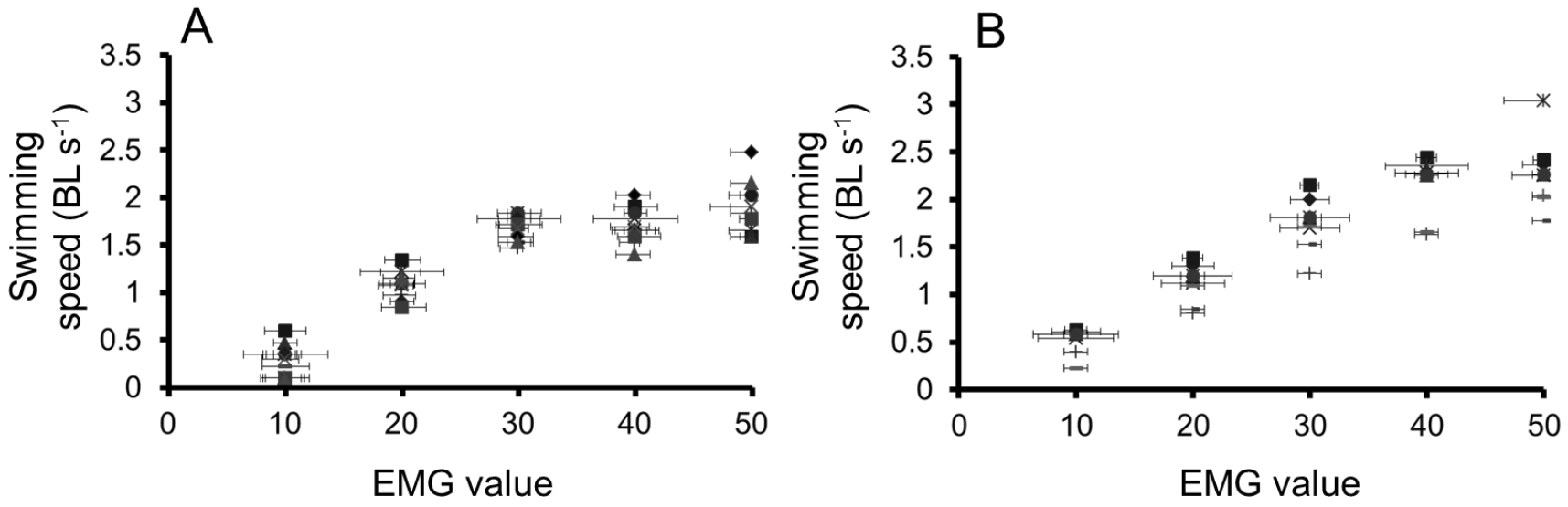

A
B
Swimming speed (BL s-1)
EMG value
0
0.5
1
1.5
2
2.5
3
3.5
0
10
20
30
40
50

Fig.7

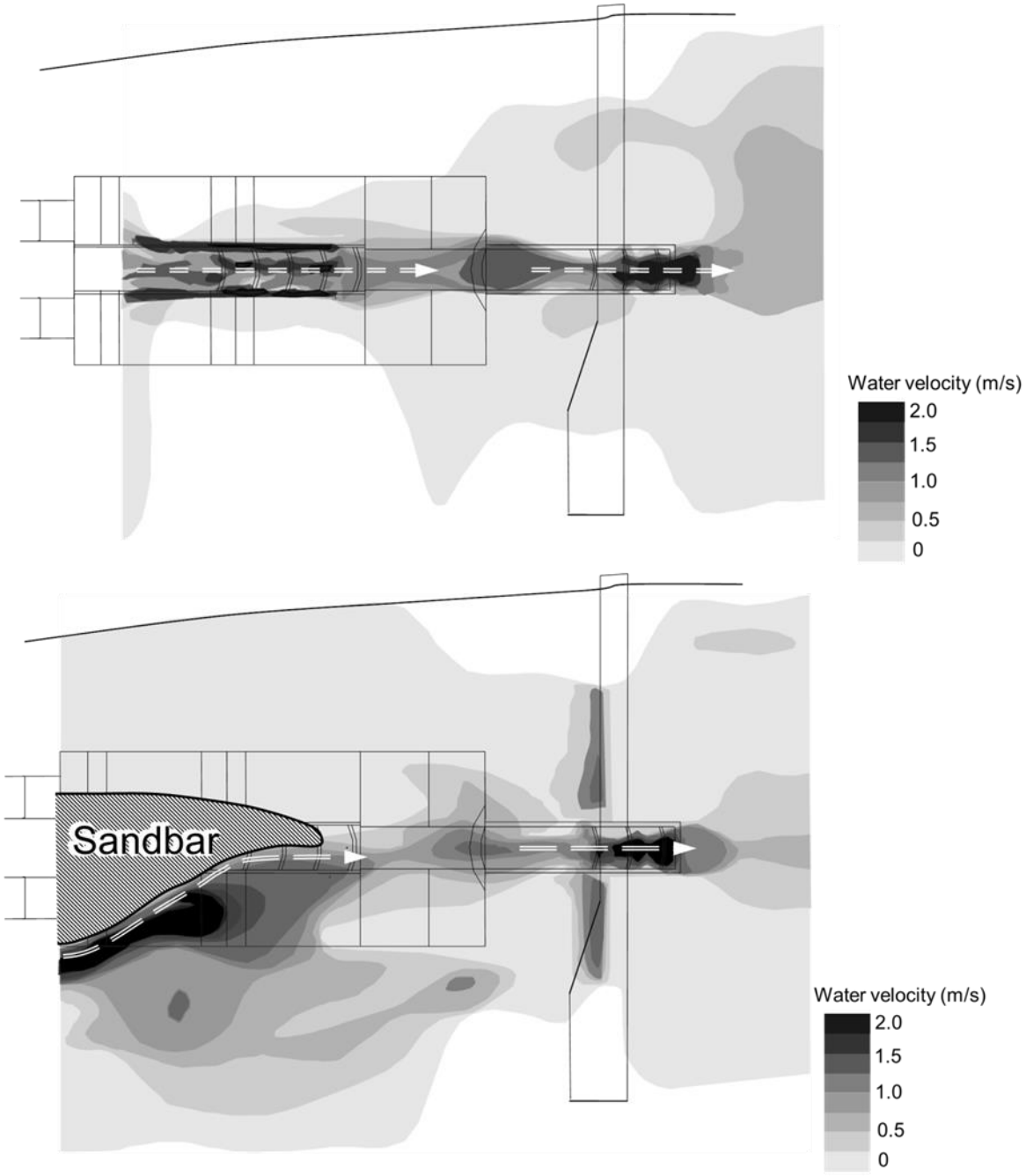

Water velocity (m/s)
2.0
1.5
1.0
0.5
0
Sandbar
Water velocity (m/s)
2.0
1.5
1.0
0.5
0

Fig.8

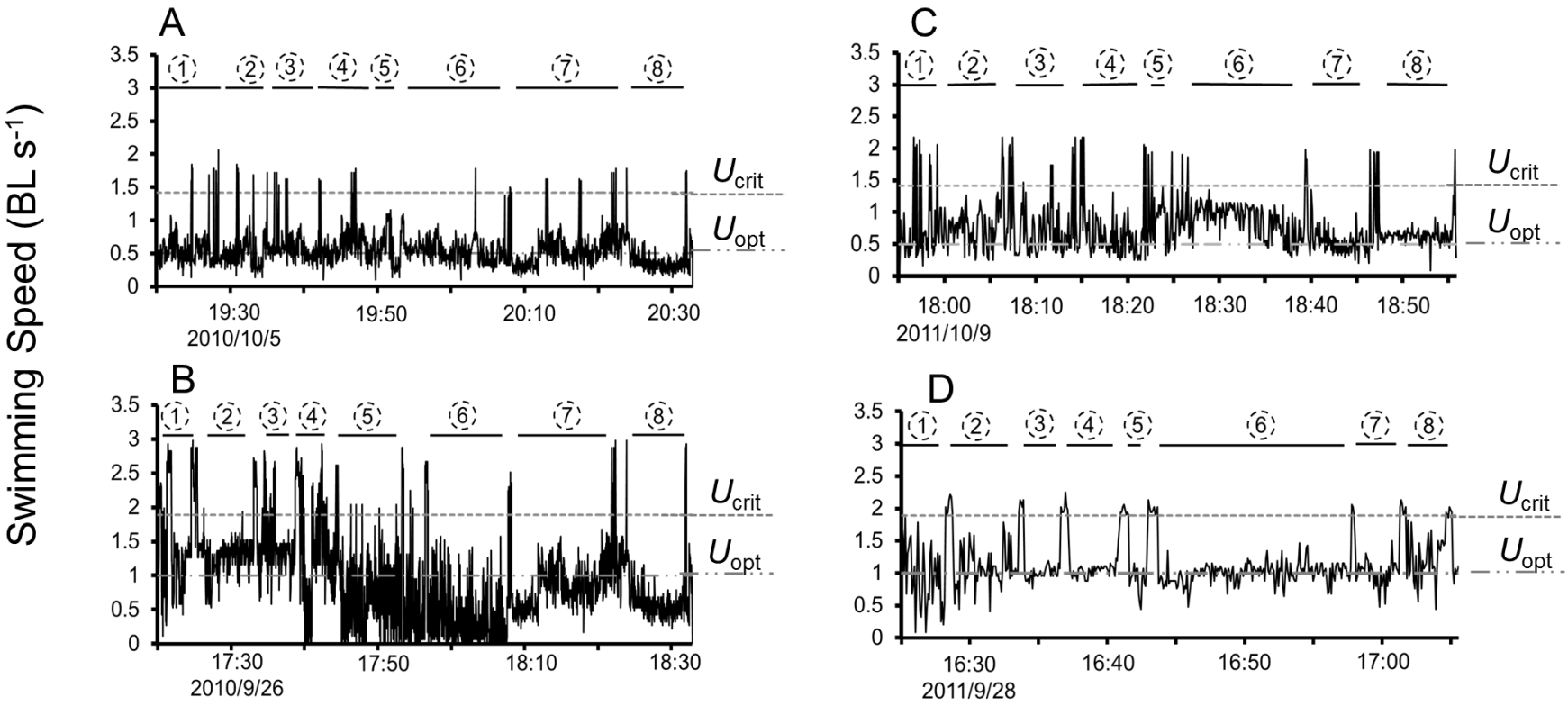
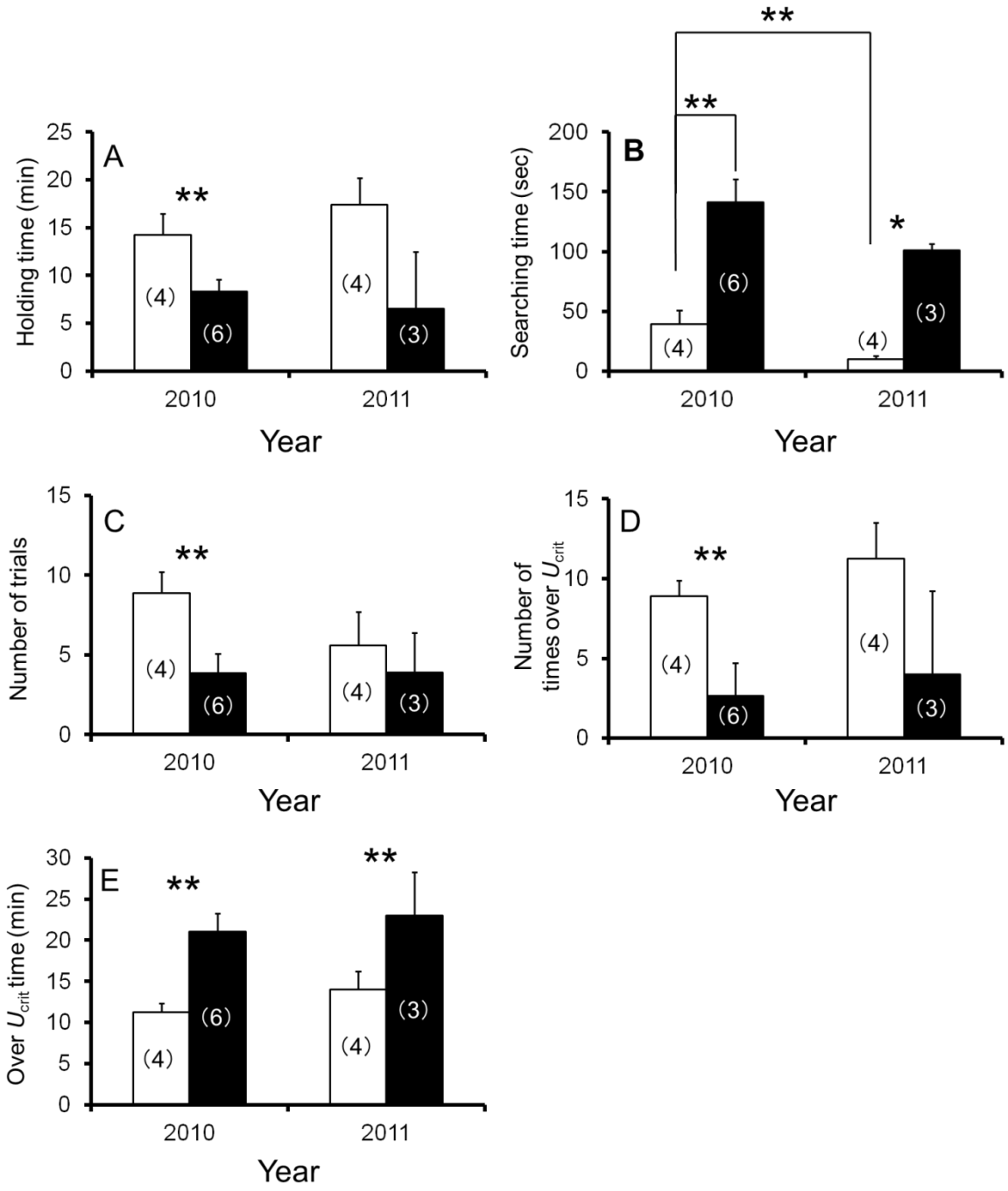

A
B
C
D
Swimming Speed (BL s-1)
Ucrit
Uopt
19:30
2010/10/5
19:50
20:10
20:30
17:30
2010/9/26
17:50
18:10
18:30
18:00
2011/10/9
18:10
18:20
18:30
18:40
18:50
16:30
2011/9/28
16:40
16:50
17:00

Fig.9


A
Holding time (min)
25
20
15
10
5
0
**
(4)
(6)
(4)
(3)
2010
2011
Year
B
Searching time (sec)
200
150
100
50
0
**
**
*
(4)
(6)
(4)
(3)
2010
2011
Year
C
Number of trials
15
10
5
0
**
(4)
(6)
(4)
(3)
2010
2011
Year
D
Number of times over U_{crit}
15
10
5
0
**
(4)
(6)
(4)
(3)
2010
2011
Year
E
Over U_{crit} time (min)
30
25
20
15
10
5
0
**
**
(4)
(6)
(4)
(3)
2010
2011
Year