



Title	Effects of anesthesia and surgery on U (crit) performance and MO ₂ in chum salmon, <i>Oncorhynchus keta</i>
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1 **Effects of anesthesia and surgery on U crit performance and MO2 in chum salmon, *Oncorhynchus keta***

2 Running title: Effects of surgery on recovery of chum salmon

3

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17

18 **Abstract**

19 Increasing threats posed by overfishing and dams to wild migratory fish make understanding their
20 migration patterns essential. Telemetry is a useful technique for elucidating salmon behaviour, but the recovery
21 periods before fish can be safely released after the attachment of telemetry devices have not yet been
22 established. Reported recovery times vary widely, from 2 h to 13 d. We examined how anaesthesia and surgery
23 to attach external electromyogram (EMG) transmitters affected chum salmon (*Oncorhynchus keta*) recovery
24 based on three physiological parameters. Fish subjected to anaesthesia plus EMG transmitter attachment
25 (EMG group), anaesthesia only (AO group), and no handling (control) were placed in a swim tunnel. Critical
26 swimming speed (U_{crit}), oxygen consumption (MO_2), and muscle activity (EMG values) were assessed 0, 1, 6,
27 12, 24, and 30 h after treatment. The MO_2 in the EMG and AO groups was higher than in the control group 1
28 h after treatment, but the U_{crit} and EMG values were not significantly different from the control group at any
29 other sampling time. We concluded that chum salmon had fully recovered their swimming ability by 1 h after
30 treatment and could be safely released into the natural environment.

31

32 **Keywords:** critical swimming speeds (U_{crit}); EMG transmitter; oxygen consumption; telemetry

33 **Introduction**

34 Understanding the migratory patterns of fish is critically important because of increasing threats posed by
35 human activities, such as overfishing and dam construction. Telemetry is a useful technique for elucidating
36 fish behaviour in the wild (McKinley and Power 1992; Økland et al. 1997; Hinch and Rand 1998; Cooke et al.
37 2004). Telemetry research on fish involves anaesthesia, surgery, and recovery, followed by either release into
38 the field for behavioural tracking or laboratory experiments (Weatherley et al. 1982; Økland et al. 1997;
39 Hinch and Bratty 2000). Following anaesthesia and surgery, all adult Pacific salmon, including sockeye
40 (*Oncorhynchus nerka* (Walbaum 1792)), masu (*O. masou* (Brevoort 1856)), pink (*O. gorbuscha* (Walbaum
41 1792)), and chum (*O. keta* (Walbaum 1792)), initially exhibit abnormal behaviour (i.e., wide gill flapping)
42 and require more than ten minutes to regain normal orientation in the water (i.e., dorsal fins positioned
43 vertically) after regaining consciousness. However, longer holding periods stress fish and result in both higher
44 mortality rates (Donaldson et al. 2011) and a greater risk of damage to or detachment of telemetry equipment
45 (Bridger and Booth 2003). Therefore, pre-spawning fish should be released as soon as possible after telemetry
46 equipment attachment.

47 Reported recovery periods after transmitter attachment range from 2 h to 13 d before release into the field
48 (Beddow and McKinley 1999; Akita et al. 2006; Enders et al. 2007; Scruton et al. 2007; Makiguchi et al.
49 2008; Pon et al. 2009; Clark et al. 2010; Cocherell et al. 2011), although some studies relied only on visual
50 observations of fish behaviour. Although there have been many reports on the physiological effects of
51 anaesthesia (Keene et al. 1998; Woody et al. 2002; Perdikaris et al. 2010), the time required for fish recovery
52 following the attachment of telemetry devices remains unresolved.

53 Transmitters can be attached externally, inserted intragastrically, or implanted into the abdominal cavity
54 of fish (Bridger and Booth 2003). External attachment causes the most hindrance to swimming (McCleave
55 and Stred 1975; Adams et al. 1998; Makiguchi and Ueda 2009), impairs swimming stability (Bridger and
56 Booth 2003), and increases oxygen consumption (Steinhausen et al. 2006). Moreover, externally-attached
57 transmitters may cause serious damage to the muscles and scales of fish (Mellas and Haynes 1985; Bridger
58 and Booth 2003). Therefore, recovery following surgery to attach an external transmitter would be expected
59 to take longer than surgery to implant other types of transmitter and can establish an upper limit on safe

60 recovery times.

61 We assumed that full recovery of fish after the attachment of telemetry devices is indicated by
62 physiologically-normal swimming activity. Therefore, this study evaluated the time required for chum salmon
63 to recover swimming ability after anaesthesia and EMG transmitter attachment; chum salmon are the most
64 popular target for fish telemetry studies in Japan (Kitahashi et al. 2000; Tanaka et al. 2005; Akita et al. 2006;
65 Makiguchi et al. 2011). The fish were physiologically assessed based on critical swimming speed (U_{crit}),
66 oxygen consumption (MO_2), and muscle activity in a swim tunnel. Our methods provide baseline data on
67 physiological recovery time in salmon after anaesthesia/surgery.

68

69 **Materials and methods**

70 *Fish capture, handling, and experimental conditions*

71 Twenty-six adult chum salmon (mean \pm SE; fork length: 62.3 ± 4.1 cm; body weight: 2.66 ± 0.61 kg) of
72 both sexes were captured using a waterwheel located about 70 km from the mouth of the Chitose River of
73 western Hokkaido, Japan, during their upstream spawning migration. Experiments were conducted at the
74 Chitose Salmon Aquarium in September and December 2010. Fish were individually transferred to compact
75 fish cages ($L \times W \times H = 1.8 \times 0.9 \times 0.6$ m) in an artificially-flowing stream. Fresh Chitose River water was
76 used in all experiments.

77 Fish were subjected to one of three treatments, each with an equal number of males and females: control
78 ($n = 12$; fork length: 61.6 ± 4.8 cm; body weight: 2.55 ± 0.64 kg), anaesthesia only (AO group; total $n = 6$;
79 fork length: 64.2 ± 4.3 cm; body weight: 3.08 ± 0.74 kg), and anaesthesia with EMG transmitter attachment
80 (EMG group; $n = 8$; fork length: 62.0 ± 2.5 cm; body weight: 2.50 ± 0.30 kg). Control fish were exposed to
81 air for a few seconds during transfer to the swim tunnel. The EMG group was anaesthetized with 0.5 ml L^{-1}
82 FA100 (eugenol; Tanabe Seiyaku, Osaka, Japan) for about 8 min, then EMG transmitters were attached
83 externally using a standard procedure developed by Makiguchi et al. (2011). Briefly, EMG transmitters
84 (CEMG-R11, Lotek Engineering, Newmarket, Ontario, Canada: 18.0 g, 16.0 mm diam., 53.0 mm long) were
85 pushed through the dorsal muscle using nylon ties, and Teflon-coated electrodes with brass muscle-anchoring
86 tips (dimension 5×1 mm) were inserted subcutaneously using a hypodermic needle at approximately $0.7 \times$

87 the body length on the left side of the fish. Paired electrode tips were positioned approximately 10 mm apart
88 and secured in the lateral red muscle toward the rear of the fish. The surgery took about 7 min, during which
89 the fish were exposed to air and their gills were irrigated. The AO group was anaesthetized as described above
90 then held in air with gill irrigation for 7 min to control for the exposure time of surgery. The anaesthetic fluid
91 was rinsed off with water, and fish were evaluated immediately after anaesthesia/surgery.

92 *Determination of critical swimming speeds (U_{crit})*

93 A swim tunnel (West Japan Fluid Engineering Laboratory Co. Ltd, Nagasaki, Japan) was used to
94 measure U_{crit} , MO_2 , and muscle activity (Fig. 1). The swim tunnel was sealed with an acrylic board to prevent
95 gas exchange, and fresh river water was pumped into it before each trial. The water temperature during all
96 experiments ranged from 12.1 to 14.7°C. Within any one experiment, water temperature varied by $\leq 1^\circ\text{C}$.

97 The U_{crit} quantifies the sub-maximum and largely aerobic swimming ability of fish and is approximately
98 the speed at which fish become fatigued during incremental velocity trials (Brett 1964, 1967; Hammer 1995).
99 Experimental fish were individually assessed for U_{crit} as a gauge of recovery. In each U_{crit} trial, the initial flow
100 velocity (V) of 0.350 body lengths (BL) s^{-1} was increased by 0.175 BL s^{-1} every 15 min until the fish were
101 fatigued and became lodged at the end of the swimming section of the tunnel. Flow velocity and the point of
102 fatigue within the terminal 15-min period were used to calculate U_{crit} , normalized for BL, as described by
103 Brett (1964):

$$104 \quad U_{crit} = U + [(T \bar{T}i^{-1}) U_i] \quad (1)$$

105 where U is the flow velocity, corrected to account for the solid blocking effects (Gehrke et al. 1990) described
106 by Bell and Terhune (1970), at which the fish last swam for the full 15-min period; U_i is the velocity
107 increment (0.175 BL s^{-1}); T is the length of time in minutes that fish were able to swim at the terminal flow
108 velocity that produced fatigue, and $\bar{T}i$ is the time between velocity increments (900 s).

109 In total, six trials were conducted, at 0, 1, 6, 12, 24, and 30 h after anaesthesia/surgery. Because each
110 U_{crit} measurement took more than an hour, the fish used in the first trial were not used again. The same
111 individuals were used in each of the second to sixth trials. In the first trial, the fish were immediately
112 measured for U_{crit} , with no acclimatization period. Before the second trial, the fish were allowed to acclimate
113 to a current velocity of $V = 0.175 \text{ m s}^{-1}$ for 1 h before the trial began. Fish were allowed to rest for ~2–3 h

114 between trials. Wagner et al. (2005) reported that fish that rested for 45 min between U_{crit} trials had similar
115 oxygen consumption values in both trials. Thus, we assumed that a resting period of 2–3 h between trials was
116 sufficient for independent measurements of U_{crit} and MO_2 .

117 *Measurement of oxygen consumption (MO_2)*

118 To measure MO_2 of fish during the trials, oxygen concentration in the swim tunnel was measured at
119 1-min intervals using a U-50 Multiparameter Water Quality Meter (Horiba Ltd., Kyoto, Japan) housed in a
120 flow-through outside the swim tunnel (Fig. 1d, e). Before the fish were introduced, the swim tunnel was
121 operated to remove air bubbles, and oxygen levels in the tunnel were replenished with fresh river water
122 between trials. Oxygen consumption per 15-min period for each fish was calculated as the difference in
123 oxygen concentration between the start and end of the period. The MO_2 ($mg\ O_2\ kg^{-1}\ h^{-1}$) for individual fish
124 during a velocity increment was calculated as $MO_2 = [O_2] v m^{-1}$, where the change in oxygen concentration
125 $[O_2]$ is measured in $mg\ O_2\ per\ l^{-1}\ h^{-1}$, v is the water volume of the swim tunnel (L), and m is the body mass of
126 the fish (kg).

127 *Measurement of EMG values*

128 Muscle activity in the EMG group was monitored with EMG transmitters. The EMG voltage was
129 calibrated and sampled at 2-s intervals. At the end of each 2-s interval, the average value was assigned a
130 unitless activity level (EMG signal) ranging from 0 to 50 and then transmitted to a radio receiver (model
131 SRX_600, Lotek Engineering Inc., Newmarket, Ontario, Canada). The mean EMG value was calculated for
132 each swimming velocity and mean and coefficient of variation (CV) were calculated for each trial and for the
133 acclimatization period.

134 *Data analysis and statistics*

135 Data are presented as the mean \pm the standard error (SE). One-factor ANOVAs were performed to assess
136 differences in U_{crit} , MO_2 , and EMG value among trials (using flow velocity as the factor) and among
137 treatments (using treatment as the factor). Control fish did not have EMG transmitters, so EMG values were
138 lacking for this group. The MO_2 data for three treatments in trials 2–6 were subsequently analysed by the
139 Tukey-Kramer test. The EMG CV was analysed using one-factor ANOVA with trial as the single factor.
140 Statistical significance was set at $P < 0.05$. Statistical analysis was performed using Excel 2007 (Microsoft,

141 Redmond, WA, USA) with the add-in Statcal3 (Yanai 2011).

142

143 **Results**

144 There were no significant differences (U_{crit} : $P > 0.05$) between the sexes in any experiment, so male and
145 female datasets were combined for each treatment.

146 *Critical swimming speed (U_{crit})*

147 The U_{crit} values for each trial are shown in Fig. 2. In the first trial, the fish in the AO and EMG groups
148 were not able to wake and swim forward for several minutes (fish remained upside down or slanted, AO
149 group: 5.13 min \pm 4.20; EMG group: 10.39 min \pm 7.08). To recover normal orientation, the fish required a
150 further 20 min after being placed in the swim tunnel. Therefore, U_{crit} could not be measured in these fish in
151 trial 1. For the control group, there were no significant differences in average U_{crit} between the first and
152 subsequent trials ($P > 0.34$ in all comparisons). No significant differences in average U_{crit} were found among
153 treatment groups in any of the subsequent trials ($P > 0.37$ in all comparisons). Thus, after anaesthesia/surgery,
154 fish regained normal swimming ability within 1 h.

155 *Oxygen consumption (MO_2)*

156 For the control group, there were no significant differences in average MO_2 between the first and
157 subsequent trials ($P > 0.17$ in all comparisons). Significant differences were found in MO_2 among all
158 treatments in trial 2 (Fig. 3; $P < 0.01$ or 0.05), but no significant differences were found in MO_2 among any
159 treatment groups in the other trials ($P > 0.09$ in all comparisons). For both AO and EMG groups, MO_2 in the
160 first trial (Fig. 3b) differed from subsequent trials (Fig. 3c–f), in which MO_2 increased with swimming speed,
161 although there were minor variations. In the AO and EMG groups, MO_2 levels were higher immediately after
162 acclimatization (at $V = 0.175$ BL s^{-1}) than at U_{crit} (Fig. 3b). Oxygen consumption in the first trial of the EMG
163 group declined over the first 1.25 h of the trial (until $V = 1.05$ BL s^{-1}), but stabilized thereafter. In the AO
164 group, MO_2 decreased over the first 30 min of the first trial (until $V = 0.525$ BL s^{-1}), then began to slowly
165 increase, as in the control. In all post-anaesthesia/surgery trials, maximum MO_2 at U_{crit} was approximately 6-7
166 mg O_2 kg^{-1} h^{-1} .

167 *EMG values*

168 Muscle activity (EMG values) in the EMG group increased with flow velocity in all trials (Fig. 4), and
169 there were no significant differences among trials ($P > 0.99$ in all comparisons). The CV of the EMG values
170 varied during the acclimatization phase more than in other phases, but no significant differences were
171 observed ($P > 0.77$ in all comparisons) in the subsequent trials (Fig. 5).

172

173 **Discussion**

174 We evaluated the time needed for chum salmon to regain full physiological swimming ability (as
175 measured by U_{crit} , MO_2 , and EMG values) after anaesthesia and surgery for EMG transmitter attachment.
176 Mean U_{crit} values were approximately 1.5 BL s^{-1} , comparable to the 1.6 BL s^{-1} reported for adult chum salmon
177 by Makiguchi et al. (2008) and for coho salmon (*O. kisutch* (Walbaum 1792)) by Lee et al. (2003). We found
178 no significant differences in mean U_{crit} values between the EMG group and either the control or AO groups in
179 any of the five trials conducted between 1–30 h after anaesthesia/surgery. We conducted similar research
180 using adult rainbow trout (*O. mykiss* (Walbaum 1792), total $n = 28$, 14 males, 14 females; mean \pm SE; fork
181 length: 52.0 ± 4.1 cm; body weight: 1.53 ± 0.36 kg) and found that swimming ability was also regained within
182 1 h after anaesthesia/surgery (unpublished data). Our fish required 5–10 min to recover normal orientation
183 after anaesthesia/surgery. In comparison, Lacroix et al. (2004) reported that juvenile Atlantic salmon began to
184 recover from anaesthesia about 2–3 min after being returned to fresh water and fully regained equilibrium and
185 darting behaviour within 60 min. Meka et al. (2003) reported that adult rainbow trout could be released
186 ~20–30 min after the start of anaesthesia/surgery, which took ~5–6 min. Obviously, the recovery period must
187 be determined for each species and life stage prior to release.

188 The MO_2 of the EMG and AO groups were substantially higher than the control 1 h after
189 anaesthesia/surgery. The fact that both groups had elevated MO_2 levels indicated that the 7 min of exposure to
190 air affected the fish. Because the decline in MO_2 stopped 1.5 h into the trial (when $V = 1.05 \text{ BL s}^{-1}$; MO_2 : 6.0),
191 we can assume that the effects of surgery had receded by this time. The MO_2 values were no longer
192 significantly different from the control at $V=0.700 \text{ BL s}^{-1}$ ($P > 0.09$). As fish swim faster, their active
193 metabolic rate increases (Brett 1964; Wagner et al. 2006), and MO_2 should increase as well. In all subsequent
194 trials, MO_2 tended to increase with flow velocity and did not differ significantly among the control, AO, and

195 EMG treatments, indicating that the fish had fully recovered from anaesthesia/surgery.

196 Maximum oxygen uptake is generally accepted to occur at U_{crit} (Farrell and Steffensen 1987), when
197 maximum aerobic capacity can be estimated (Hammer 1995). In none of our trials did the MO_2 values at U_{crit}
198 differ among treatments. Moreover, the increase in MO_2 appeared to slow or even reverse immediately before
199 U_{crit} was reached, similar to findings in chinook salmon (Geist et al. 2003). In all cases, the EMG group
200 consumed substantially more oxygen 1 h after anaesthesia/surgery than in subsequent trials, but because
201 neither U_{crit} nor MO_2 at U_{crit} differed from the control in the first trial, we concluded that the elevated MO_2
202 value did not affect swimming activity.

203 In all post-surgery trials, EMG values in the EMG group increased with flow velocity, in agreement with
204 the report of Makiguchi et al. (2011) demonstrating that EMG values in chum salmon increased with
205 swimming speed. There were no significant differences in average EMG values among trials. These results
206 indicate that muscular activity in fish attached with EMG transmitters had recovered to normal levels within 1
207 h of anaesthesia/surgery. In addition, no significant differences in the EMG value CV were found among
208 trials. During the acclimatization period (0–1 h) when the fish were waking, there was substantial variation in
209 EMG values.

210 This study provided clear evidence that chum salmon that migrated to the Chitose River to spawn
211 recovered within 1 h from both anaesthesia and surgery to attach external EMG transmitters, as indicated by
212 three physiological measures, normal swimming behaviour, U_{crit} , MO_2 , and EMG values. Their swimming
213 ability remained stable thereafter. Thus, we concluded that chum salmon can be used for telemetry
214 experiments 1 h after the attachment of an external transmitter without significant physiological disability.
215 Our findings are likely to apply to intragastric and abdominally-implanted transmitters as well, because
216 external transmitters are more likely to affect swimming ability (McCleave and Stred 1975; Adams et al.
217 1998; Makiguchi and Ueda 2009). Thorstad et al. (2000) reported no differences in swimming endurance of
218 adult Atlantic salmon among control fish, those with small or large external dummy transmitters, or fish with
219 surgical implants.

220 The importance of telemetry in understanding fish migration ensures that the number of telemetry studies
221 will continue to increase as the devices become more compact and affordable. A variety of anaesthetics and

222 equipment will be used on different species in different conditions, including water temperature, and fish age
223 class (e.g., young, adult, spawning), and behavioural phase (e.g., downstream versus upstream migration), that
224 might affect recovery time. Pike, for example, recovered quickly when anesthetized at 12°C, but required
225 several hours to fully recover when anaesthetized at temperatures of <2°C (Jepsen et al. 2001). Our method
226 should prove practical in evaluating a range of species under many different conditions. We are convinced
227 that proper use of telemetry, including reasonable recovery and release times, will yield high quality data that
228 will help to resolve various problems for migrating salmon, including fishways (Roscoe et al. 2011), dams
229 (Cocherell et al. 2011), and global climate change (Hasler et al. 2012).

230 In summary, the current research showed that chum salmon had fully recovered from surgery to attach
231 external telemetry equipment within 1 h. This study was the first to attempt to understand the physiological
232 effects of anaesthesia/surgery on the recovery of chum salmon. The results provided baseline information on
233 appropriate release times for chum salmon after the attachment of telemetry devices. Furthermore, our
234 methods should be widely applicable to other species, types of telemetry device, and environmental
235 conditions.

236

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242

243 **References**

- 244 Adams NS, Rondorf DW, Evans SD, Kelly JE, Perry RW (1998) Effects of surgically and gastrically
245 implanted radio transmitters on swimming performance and predator avoidance of juvenile chinook
246 salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 55 (4):781-787
- 247 Akita M, Makiguchi Y, Nii H, Nakao K, Sandahl JF, Ueda H (2006) Upstream migration of chum salmon
248 through a restored segment of the Shibetsu River. Ecol Freshw Fish 15 (2):125-130. doi:DOI
249 10.1111/j.1600-0633.2006.00153.x
- 250 Beddow TA, McKinley RS (1999) Importance of electrode positioning in biotelemetry studies estimating
251 muscle activity in fish. J Fish Biol 54 (4):819-831
- 252 Bell WM, Terhune LDB (1970) Water tunnel design for fisheries research. Technical Report Fisheries
253 Research Board of Canada 195:1-69
- 254 Brett JR (1964) The respiratory metabolism and swimming performance of young sockeye salmon. Journal of
255 the Fisheries Research Board of Canada 21:1183-1226
- 256 Brett JR (1967) Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue
257 time and temperature. Journal of Fisheries Research Board of Canada 24:1731-1741
- 258 Bridger CJ, Booth RK (2003) The effects of biotelemetry transmitter presence and attachment procedures on
259 fish physiology and behavior. Rev Fish Sci 11 (1):13-34
- 260 Clark TD, Sandblom E, Hinch SG, Patterson DA, Frappell PB, Farrell AP (2010) Simultaneous biologging of
261 heart rate and acceleration, and their relationships with energy expenditure in free-swimming
262 sockeye salmon (*Oncorhynchus nerka*). Journal of Comparative Physiology B-Biochemical Systemic
263 and Environmental Physiology 180 (5):673-684. doi:10.1007/s00360-009-0442-5
- 264 Cocherell SA, Cocherell DE, Jones GJ, Miranda JB, Thompson LC, Cech JJ, Klimley AP (2011) Rainbow
265 trout *Oncorhynchus mykiss* energetic responses to pulsed flows in the American River, California,
266 assessed by electromyogram telemetry. Environ Biol Fishes 90 (1):29-41.
267 doi:10.1007/s10641-010-9714-x
- 268 Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG, Butler PJ (2004) Biotelemetry: a
269 mechanistic approach to ecology. Trends Ecol Evol 19 (6):334-343. doi:10.1016/j.tree.2004.04.003

270 Donaldson MR, Hinch SG, Patterson DA, Hills J, Thomas JO, Cooke SJ, Raby GD, Thompson LA,
271 Robichaud D, English KK, Farrell AP (2011) The consequences of angling, beach seining, and
272 confinement on the physiology, post-release behaviour and survival of adult sockeye salmon during
273 upriver migration. *Fish Res* 108 (1):133-141. doi:10.1016/j.fishres.2010.12.011

274 Enders EC, Clarke KD, Pennell CJ, Ollerhead LMN, Scruton DA (2007) Comparison between PIT and radio
275 telemetry to evaluate winter habitat use and activity patterns of juvenile Atlantic salmon and brown
276 trout. *Hydrobiologia* 582:231-242. doi:DOI 10.1007/s10750-006-0562-9

277 Farrell AP, Steffensen JF (1987) An analysis of the energetic cost of the branchial and cardiac pumps during
278 sustained swimming in trout. *Fish Physiol Biochem* 4 (2):73-79

279 Gehrke PC, Fidler LE, Mense DC, Randall DJ (1990) A respirometer with controlled water-quality and
280 computerized data acquisition for experiments with swimming fish. *Fish Physiol Biochem* 8
281 (1):61-67

282 Geist DR, Brown RS, Cullinan VI, Mesa MG, Vanderkooi SP, McKinstry CA (2003) Relationships between
283 metabolic rate, muscle electromyograms and swim performance of adult chinook salmon. *J Fish Biol*
284 63 (4):970-989. doi:DOI 10.1046/j.1095-8649.2003.00217.x

285 Hammer C (1995) Fatigue and exercise tests with fish. *Comparative Biochemistry and Physiology*
286 a-Physiology 112 (1):1-20

287 Hasler CT, Cooke SJ, Hinch SG, Guimond E, Donaldson MR, Mossop B, Patterson DA (2012) Thermal
288 biology and bioenergetics of different upriver migration strategies in a stock of summer-run Chinook
289 salmon. *J Therm Biol* 37 (4):265-272. doi:10.1016/j.jtherbio.2011.02.003

290 Hinch SG, Bratty J (2000) Effects of swim speed and activity pattern on success of adult sockeye salmon
291 migration through an area of difficult passage. *Trans Am Fish Soc* 129 (2):598-606

292 Hinch SG, Rand PS (1998) Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus*
293 *nerka*): role of local environment and fish characteristics. *Can J Fish Aquat Sci* 55 (8):1821-1831

294 Jepsen N, Beck S, Skov C, Koed A (2001) Behavior of pike (*Esox lucius* L.) > 50 cm in a turbid reservoir and
295 in a clearwater lake. *Ecol Freshw Fish* 10 (1):26-34. doi:10.1034/j.1600-0633.2001.100104.x

296 Keene JL, Noakes DLG, Moccia RD, Soto CG (1998) The efficacy of clove oil as an anaesthetic for rainbow

297 trout, *Oncorhynchus mykiss* (Walbaum). Aquac Res 29 (2):89-101

298 Kitahashi T, Ando H, Urano A, Ban M, Saito S, Tanaka H, Naito Y, Ueda H (2000) Micro data logger
299 analyses of homing behavior of chum salmon in Ishikari Bay. Zoological Science 17 (9):1247-1253

300 Lacroix GL, Knox D, McCurdy P (2004) Effects of implanted dummy acoustic transmitters on juvenile
301 Atlantic salmon. Trans Am Fish Soc 133 (1):211-220

302 Lee CG, Farrell AP, Lotto A, Hinch SG, Healey MC (2003) Excess post-exercise oxygen consumption in
303 adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon following critical speed
304 swimming. J Exp Biol 206 (18):3253-3260. doi:Doi 10.1242/Jeb.00548

305 Makiguchi Y, Konno Y, Konishi K, Miyoshi K, Sakashita T, Nii H, Nakao K, Ueda H (2011) EMG telemetry
306 studies on upstream migration of chum salmon in the Toyohira river, Hokkaido, Japan. Fish Physiol
307 Biochem 37 (2):273-284. doi:10.1007/s10695-011-9495-y

308 Makiguchi Y, Nii H, Nakao K, Ueda H (2008) Migratory behaviour of adult chum salmon, *Oncorhynchus*
309 *keta*, in a reconstructed reach of the Shibetsu River, Japan. Fish Manag Ecol 15 (5-6):425-433.
310 doi:DOI 10.1111/j.1365-2400.2008.00632.x

311 Makiguchi Y, Ueda H (2009) Effects of external and surgically implanted dummy radio transmitters on
312 mortality, swimming performance and physiological status of juvenile masu salmon *Oncorhynchus*
313 *masou*. J Fish Biol 74 (1):304-311

314 McCleave JD, Stred KA (1975) Effect of dummy telemetry transmitters on stamina of Atlantic salmon (*Salmo*
315 *salar*) smolts. Journal of the Fisheries Research Board of Canada 32:559-563

316 McKinley RS, Power G (1992) Measurement of activity and oxygen consumption for adult lake sturgeon
317 (*Acipenser fulvescens*) in the wild using radio-transmitted EMG signals. In: Priede AG, Swift SM
318 (eds) Wildlife Telemetry: Remote Monitoring and Tracking Animals, vol 307. Ellis Horwood, West
319 Sussex, U.K.,

320 Meka JM, Knudsen EE, Douglas DC, Benter RB (2003) Variable migratory patterns of different adult
321 rainbow trout life history types in a southwest Alaska watershed. Trans Am Fish Soc 132
322 (4):717-732

323 Mellas EJ, Haynes JM (1985) Swimming performance and behavior of rainbow-trout (*Salmo gairdneri*) and

324 white perch (*Morone Americana*) - effects of attaching telemetry transmitters. Can J Fish Aquat Sci
325 42 (3):488-493

326 Økland F, Finstad B, McKinley RS, Thorstad EB, Booth RK (1997) Radio-transmitted electromyogram
327 signals as indicators of physical activity in Atlantic salmon. J Fish Biol 51 (3):476-488

328 Perdikaris C, Nathanailides C, Gouva E, Gabriel UU, Bitchava K, Athanasopoulou F, Paschou A, Paschos I
329 (2010) Size-relative Effectiveness of Clove Oil as an Anaesthetic for Rainbow Trout (*Oncorhynchus*
330 *mykiss* Walbaum, 1792) and Goldfish (*Carassius auratus* Linnaeus, 1758). Acta Vet Brno 79
331 (3):481-490. doi:10.2754/avb201079030481

332 Pon LB, Hinch SG, Cooke SJ, Patterson DA, Farrell AP (2009) Physiological, energetic and behavioural
333 correlates of successful fishway passage of adult sockeye salmon *Oncorhynchus nerka* in the Seton
334 River, British Columbia. J Fish Biol 74 (6):1323-1336. doi:10.1111/j.1095-8649.2009.02213.x

335 Roscoe DW, Hinch SG, Cooke SJ, Patterson DA (2011) Fishway passage and post-passage mortality of
336 up-river migrating sockeye salmon in the Seton River, British Columbia. River Res Appl 27
337 (6):693-705. doi:10.1002/rra.1384

338 Scruton DA, Booth RK, Pennell CJ, Cubitt F, McKinley RS, Clarke KD (2007) Conventional and EMG
339 telemetry studies of upstream migration and tailrace attraction of adult Atlantic salmon at a
340 hydroelectric installation on the Exploits River, Newfoundland, Canada. Hydrobiologia 582:67-79.
341 doi:DOI 10.1007/s10750-006-0558-5

342 Steinhausen MF, Andersen NG, Steffensen JF (2006) The effect of external dummy transmitters on oxygen
343 consumption and performance of swimming Atlantic cod. J Fish Biol 69 (3):951-956. doi:DOI
344 10.1111/j.1095-8649.2006.01143.x

345 Tanaka H, Naito Y, Davis ND, Urawa S, Ueda H, Fukuwaka M (2005) First record of the at-sea swimming
346 speed of a Pacific salmon during its oceanic migration. Marine Ecology-Progress Series 291:307-312.
347 doi:10.3354/meps291307

348 Thorstad EB, Økland F, Finstad B (2000) Effects of telemetry transmitters on swimming performance of adult
349 Atlantic salmon. J Fish Biol 57 (2):531-535. doi:DOI 10.1006/jfbi.2000.1315

350 Wagner GN, Hinch SG, Kuchel LJ, Lotto A, Jones SRM, Patterson DA, Macdonald JS, Kraak GVD,

351 Shrimpton M, English KK, Larsson S, Cooke SJ, Healey MC, Farrell AP (2005) Metabolic rates and
352 swimming performance of adult Fraser River sockeye salmon (*Oncorhynchus nerka*) after a
353 controlled infection with *Parvicapsula minibicornis*. Can J Fish Aquat Sci 62 (9):2124-2133.
354 doi:10.1139/f05-126

355 Wagner GN, Kuchel LJ, Lotto A, Patterson DA, Shrimpton JM, Hinch SG, Farrell AP (2006) Routine and
356 active metabolic rates of migrating adult wild sockeye salmon (*Oncorhynchus nerka* Walbaum) in
357 seawater and freshwater. Physiol Biochem Zool 79 (1):100-108

358 Weatherley AH, Rogers SC, Pincock DG, Patch JR (1982) Oxygen consumption of active rainbow trout,
359 *Salmo gairdneri* Richardson, derived from electromyograms obtained by radiotelemetry. J Fish Biol
360 20 (4):479-489

361 Woody CA, Nelson J, Ramstad K (2002) Clove oil as an anaesthetic for adult sockeye salmon: field trials. J
362 Fish Biol 60 (2):340-347. doi:10.1006/jfbi.2001.1842

363 Yanai H (2011) Statcel – The useful add-in software forms on Excel (3rd ed). OMS, Tokyo, Japan
364
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366 **Figure Legends**

367 **Fig. 1** Swim tunnel used in the swimming trials (length: 1.5 m; diam.: 0.3 m). Water flow was generated
368 using a voltage-controlled motor and propeller, with the voltage calibrated against flow velocity. (a)
369 Anticlockwise water flow with a water volume of 450 L. (b) Swimming area (L = 1.5 m). (c) Water
370 quality sensor. (d) Water quality indicator/data logger. (e) Flow velocity controller. (f) Voltage-controlled
371 motor and propeller. (g) Cooler. The water temperature was set at 12°C

372

373 **Fig. 2.** Relationship between the trials after anaesthesia/surgery and U_{crit} in chum salmon (N = 6–12 per
374 treatment). Immediately after anaesthesia/surgery, fish in the anaesthesia only (AO) and EMG transmitter
375 attachment (EMG) groups could not swim, so their U_{crit} could not be measured in the first trial at 0 h.
376 Subsequent trials were begun 1, 6, 12, 24, and 30 h after anaesthesia/surgery. None of the measured U_{crit}
377 values were significantly different from any other ($P > 0.05$).

378

379 **Fig. 3.** Relationship between flow velocity and oxygen consumption (N = 6–12 per treatment). Immediately
380 after anaesthesia/surgery, fish in the anaesthesia only (AO) and EMG transmitter attachment (EMG)
381 groups could not swim, so their MO_2 could not be measured in the first trial at 0 h. Subsequent trials were
382 begun 1, 6, 12, 24, and 30 h after anaesthesia/surgery. Except in trial 2 (begun 1 h after
383 anaesthesia/surgery), oxygen consumption increased with flow velocity. For trial 2, significant
384 differences were found until $V = 0.525 \text{ BL s}^{-1}$ ($*P < 0.05$, $**P < 0.01$ by one-factor ANOVA followed by
385 the Tukey-Kramer test).

386

387 **Fig. 4.** Relationship between flow velocity and muscle activity (EMG value) in fish with externally-attached
388 EMG transmitters (N = 8). Trials were begun 1, 6, 12, 24, and 30 h after anaesthesia/surgery. For each
389 flow velocity in each trial, five EMG values were averaged. Muscle activity increased with flow velocity
390 in all trials, and no significant differences were observed among trials at each flow velocity ($P > 0.05$).

391

392 **Fig. 5.** Relationship between the trials after anaesthesia/surgery and the mean coefficient of variation (CV) of

393 the EMG value. Although substantial variation in the EMG CV occurred during the acclimatization
394 period (~0–1 h) after anaesthesia/surgery, no significant differences were observed in EMG CV ($P >$
395 0.05).
396

397 **Fig. 1**

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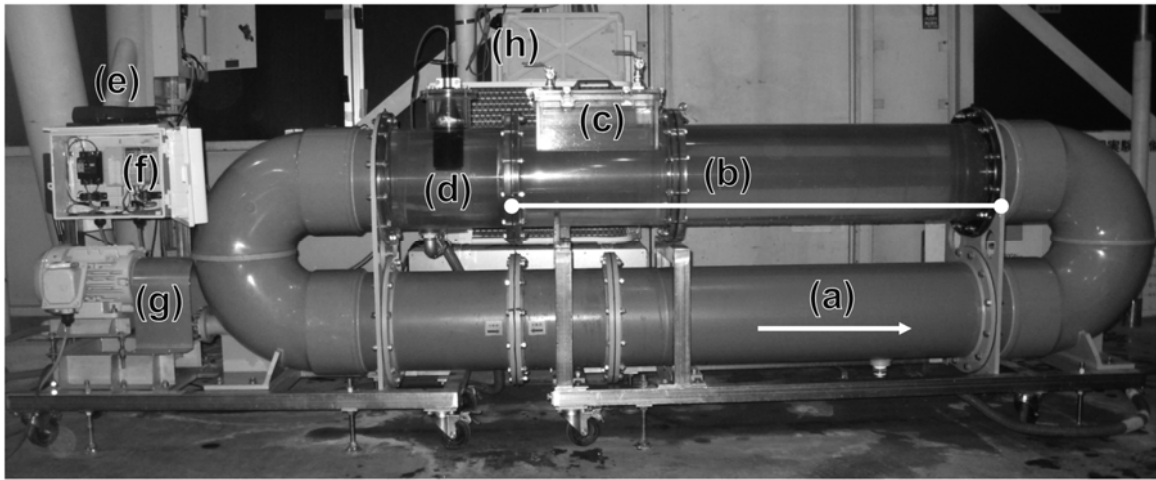
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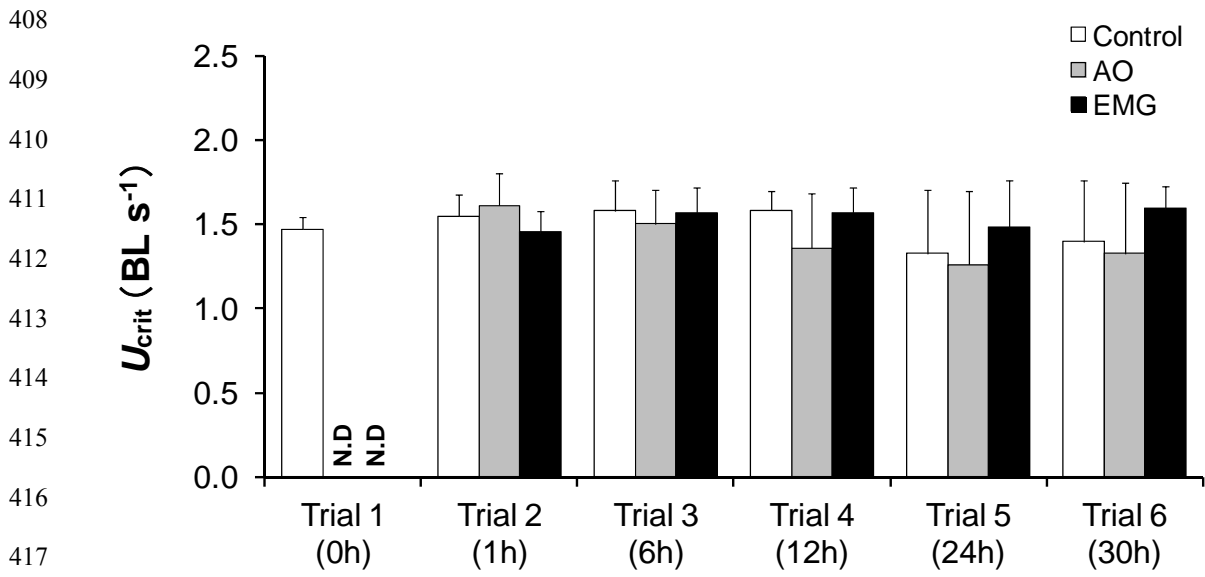
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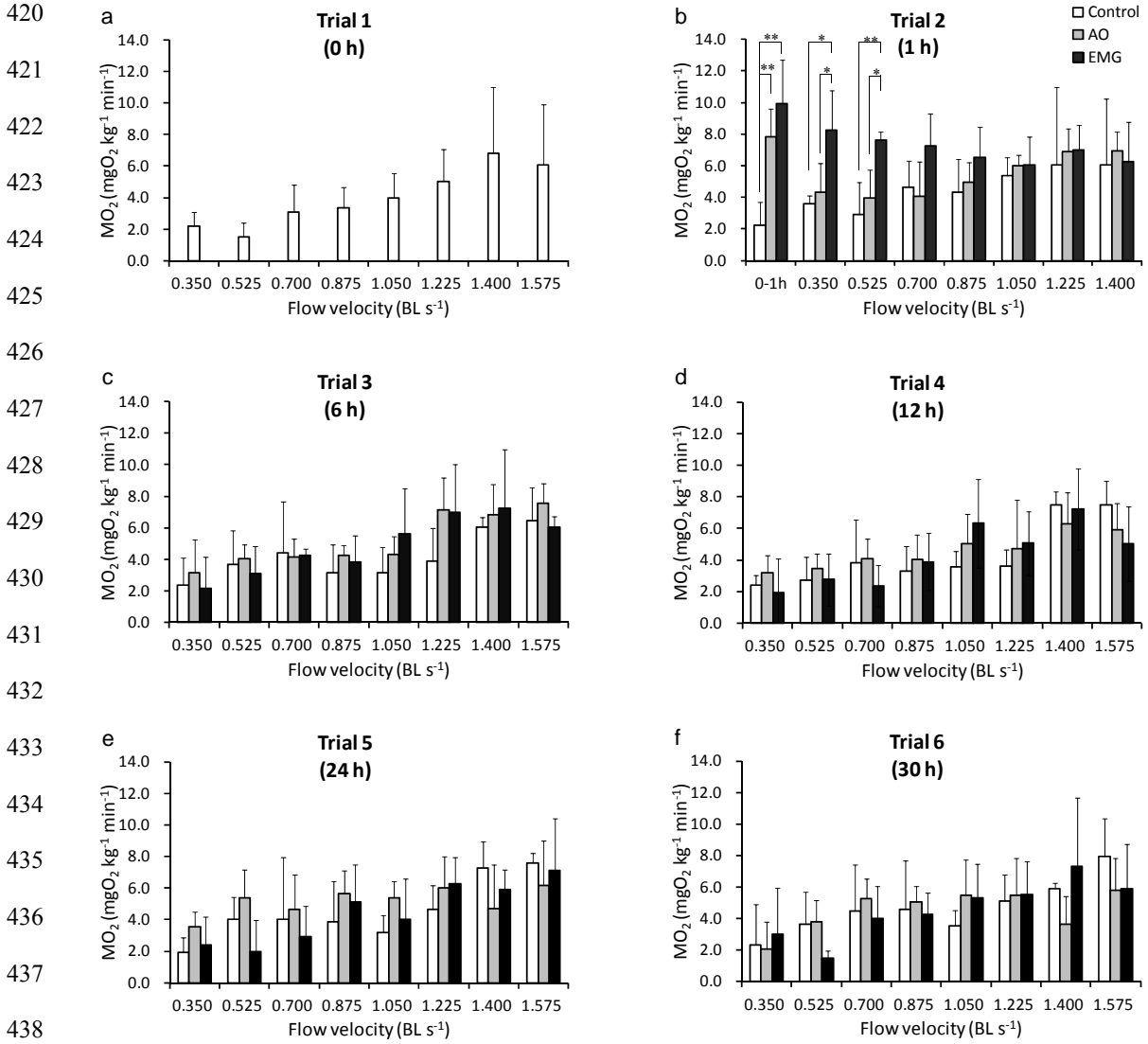
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407 **Fig. 2**

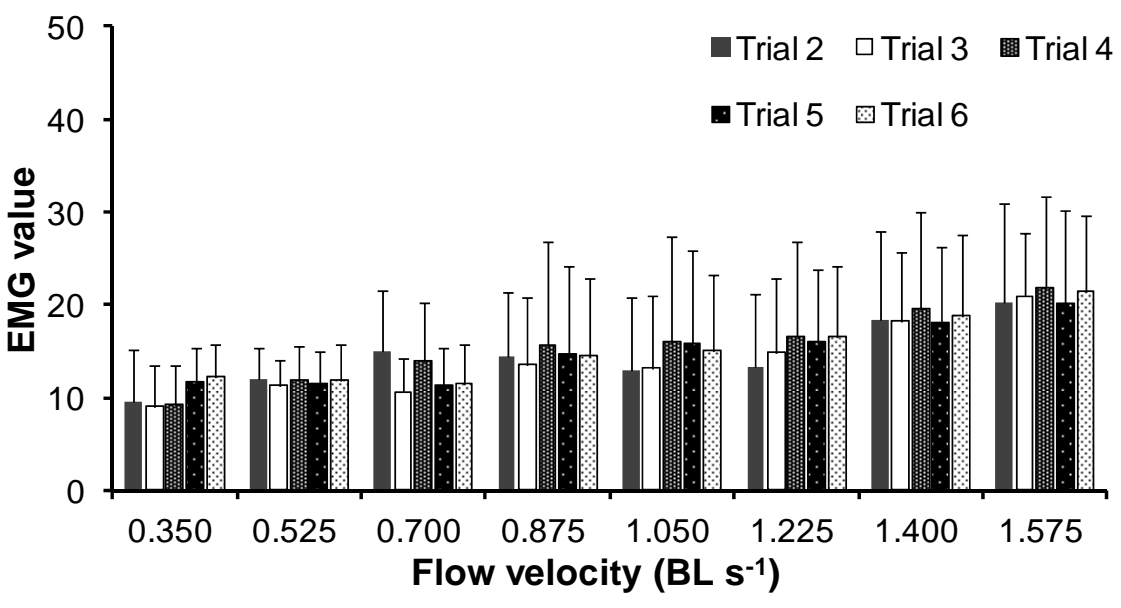


419 **Fig. 3**



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Fig. 4



452 **Fig. 5**

