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# Calibrating acoustic acceleration transmitters for estimating energy use by wild adult Pacific salmon

S.M. Wilson [a,b,*], S.G. Hinch [c], E.J. Eliason [c,d], A.P. Farrell [d], S.J. Cooke [a,b]

[a] Fish Ecology and Conservation Physiology Laboratory, Ottawa-Carleton Institute for Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6
[b] Institute of Environmental Science, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6
[c] Center for Applied Conservation Research, Forest Sciences Centre, University of British Columbia, Vancouver, BC, Canada V6T 1Z4
[d] Department of Zoology and Faculty of Land and Food Systems, University of British Columbia, 6270 University Boulevard, Vancouver, BC, Canada V6T 1Z4

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ABSTRACT

This study is the first to calibrate acceleration transmitters with energy expenditure using a vertebrate model species. We quantified the relationship between acoustic accelerometer output and oxygen consumption across a range of swim speeds and water temperatures for Harrison River adult sockeye salmon (*Oncorhynchus nerka*). First, we verified that acceleration transmitters with a sampling frequency of 10 Hz could be used as a proxy for movement in sockeye salmon. Using a mixed effects model, we determined that tailbeat frequency and acceleration were positively correlated ($p<0.0001$), independent of tag ID. Acceleration ($p<0.0001$) was positively related to swim speed while fork length ($p=0.051$) was negatively related to swim speed. Oxygen consumption and accelerometer output ($p<0.0001$) had a positive linear relationship and were temperature dependent ($p<0.0001$). There were no differences in swim performance ($F_{2,12}=1.023$, $p=0.820$) or oxygen consumption ($F_{1,12}=0.054$, $p=0.332$) between tagged and untagged individuals. Five tagged fish were released into the Fraser River estuary and manually tracked. Of the five fish, three were successfully tracked for 1 h. The above relationships were used to determine that the average swim speed was $1.25\pm0.03$ body lengths $s^{-1}$ and cost of transport was $3.39\pm0.17$ mg $O_2$ $kg^{-1}$ $min^{-1}$, averaged across the three detected fish. Acceleration transmitters can be effectively used to remotely evaluate fine-scale behavior and estimate energy consumption of adult Pacific salmon throughout their homeward spawning migration.



## 1. Introduction

Understanding energy use is fundamental to the study of animal physiology, behavior and evolutionary ecology since the energetic costs of various activities can influence fitness (McNamara and Houston, 1996). Unfortunately, estimating energy use through measuring metabolic rate ($MO_2$) in a natural setting has proven difficult, particularly in aquatic organisms. Doubly-labeled water and the heart rate method are the two main methods for the estimation of field metabolic rate in birds and mammals; though both have several well-documented limitations (see review by Butler et al., 2004). However, the doubly-labeled water method has limited applicability in fish because water flux through skin can create errors of up to 50% (Nagy and Costa, 1980). Similarly, the heart rate method, which depends on a reliable relationship between heart rate and $MO_2$ suffers in fishes because of the highly variable cardiac stroke volume with physiological state, consequently decreasing the accuracy of the estimate of $MO_2$ (Scharold and Gruber, 1991; Thorarensen et al., 1996). Thus, alternative methods are required to determine metabolic rate and estimate energy use in a natural setting.

Movement has been successfully used as a proxy for energy use in fish, with tailbeat frequency (TBF) (e.g. Brett, 1965, 1995; Hinch and Rand, 1998; Lowe et al., 1998) and swim speed (e.g. Brown et al., 2007; Payne et al., 2011) both being well correlated with $MO_2$. In nature, integration of TBF and locomotory effort is possible in fish using electromyogram (EMG) telemetry, which sums the electrical impulses of the caudal axial musculature and has been correlated with TBF and swim speed in controlled swim flume experiments. This technique has been used successfully in a number of field studies (reviewed in Cooke et al., 2004b), but like heart rate biotelemetry it requires surgical implantation of electrodes, which increases handling time and stress (Cooke et al., 2004a, 2004b). Some studies suggest that individual EMG tags require calibration with swim speed because slight variations in electrode placement can significantly affect the EMG output and hence its relationship with swim speed (Beddow and McKinley, 1999; Geist et al., 2002). In addition, most EMG studies have involved radio tags, which are limited to use in freshwater environments, and although acoustic EMG tags are available for use in seawater (Lembo et al., 2008), the need to calibrate the tags remains.

* Corresponding author at: 4630 CTTC, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6. Tel.: +1 613 302 1278; fax: +1 613 520 3539.
*E-mail address:* swilson471@gmail.com (S.M. Wilson).

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Given the above concerns, accelerometer sensors are being posited as an alternative for measuring energy expenditure in fishes. Similar to EMG technology, accelerometer sensors rely on the relationship between swimming activities and energy expenditure (see Halsey et al., 2011). Accelerometer loggers can measure acceleration at high frequencies (>100 Hz) in up to three axes, providing high-resolution data. Already, they have been successfully used to establish relationships with high correlation coefficients ($R^2$) between $MO_2$ and three dimensional (Overall Dynamic Body Acceleration (ODBA)) or two dimensional (Partial Dynamic Body Acceleration (PDBA)) acceleration (Shepard et al., 2008) in a wide range of taxa (e.g. humans: Halsey et al., 2008; birds: Wilson et al., 2006; Green et al., 2009), including fishes (sharks: Gleiss et al., 2010, salmon: Clark et al., 2010). However, as with all loggers, they have limited applicability for use in a natural environment where it is more difficult to retrieve loggers (Cooke et al., 2004a). Due to many logistical constraints, high costs of working in marine environments, and the need to retrieve tags, studies looking at movement of marine animals have been limited.

The development of an acoustic acceleration transmitter allows for transmission of data, rather than storing data that must be later retrieved and downloaded. Acceleration transmitters report acceleration at a lower sampling frequency (typically 10 Hz) than in loggers and calculate root mean square (RMS) acceleration (henceforth referred to as acceleration) to minimize battery drain when transmitting data. This new technology has been used to monitor fine scale movement patterns in great barracuda, *Sphyraena barracuda* (O'Toole et al., 2010) and estimate energy use of bonefish, *Albula vulpes* (Murchie et al., 2011) and cuttlefish, *Sepia apama* (Payne et al., 2011). However, only Payne et al. (2011) used a swim flume to perform controlled calibrations between accelerometer output and $MO_2$, finding non-linear correlations between acceleration and both swim speed and $MO_2$ for the invertebrate cuttlefish. To date, no studies have calibrated the relationship between $MO_2$ and acceleration transmitter output for any vertebrate. Development of species- and life-stage-specific relationships between $MO_2$ and acceleration is required before acceleration transmitters can be used to accurately estimate energy expenditure in free-swimming aquatic organisms.

Although sockeye salmon (*Oncorhynchus nerka*) are the most well-studied of the Pacific salmonids (Hinch et al., 2006), study of their energy expenditure and overall energy requirements has been limited, particularly in the marine environment (Drenner et al., 2012). Indeed, energetic budgets for ocean migration simplistically determine average swim speed by dividing the distance traveled by the time between release and re-capture, an estimate that fails to account for changes in energetic demands due to currents and tides (Quinn et al., 1989). Furthermore, energy budgets based on EMG biotelemetry in freshwater have used short river sections and small sample sizes (Hinch and Rand, 1998; Rand and Hinch, 1998; Hinch and Bratty, 2000). Therefore, acoustic acceleration transmitters could find immediate application to follow sockeye salmon migrations in both marine and freshwater environments.

Before research on free-swimming sockeye salmon using the acoustic acceleration transmitters can begin, the relationship between movement and body acceleration, as determined by the new acceleration transmitter, must be validated for use in sockeye salmon. Furthermore, a relationship between acceleration and rate of $MO_2$ at different temperatures would be required for accurate estimates of energy in the field. Therefore, the objectives of the present study were to determine: (1) if transmitting accelerometers using a 10 Hz sampling frequency accurately relayed information on swimming activity in adult sockeye salmon (*O. nerka*); (2) the relationship between accelerometer output and swimming speed, (3) the relationship between accelerometer output and $MO_2$ across a range of ecologically relevant temperatures, and (4) a proof-of-principle use of these accelerometers in a natural setting.

## 2. Materials and methods

### 2.1. Fish collection

This study was conducted in accordance with the guidelines of the Canadian Council of Animal Care, as administered by Carleton University (Animal Care #B10-06) and the University of British Columbia (Animal Care #A11-0212). Seventeen Harrison River sockeye salmon (*O. nerka*) were used for this study (10 males and 7 females; fork length (FL) = 57.7–68.9 cm). Harrison River sockeye salmon were captured on September 26th, 2011 by beach seine on the Harrison River (49° 17′N, 121° 54′W) during their freshwater migration to natal spawning areas. They were transported by truck (~60 km) to the Cultus Lake Salmon Research Laboratory (Fisheries and Oceans Canada), where each individual was tagged with a passive integrated transponder. Two scales were removed for population identification via scale analysis (Cook and Guthrie, 1987), and to ensure fish were of the Harrison River sockeye salmon population. Prior to the swim trials, fish were held in outdoor freshwater circular tanks (1400 L) for 3–22 days under seasonal photoperiod at a water speed of 0.30 m $s^{-1}$ and a water temperature of 10.8 °C–12.9 °C. Sex was determined by dissection after swim trials were complete. Salmon were not fed, as they naturally cease feeding prior to river entry (at least one week prior to capture).

### 2.2. Swim trial

Swim trials were completed on October 1st–20th, 2011 using two Brett-style swim tunnel respirometers (fully described in Jain et al., 1997 and Lee et al., 2003). To encourage steady swimming, the first 100 cm of the 'upstream' portion of each swim tunnel was covered with black plastic, except for a single strip along the bottom of the tunnel to allow for observation of TBF. Approximately 10–12 h prior to the first swim trial, each individual was anaesthetized with MS222 (0.1 g $L^{-1}$ in 0.2 g $L^{-1}$ $NaHCO_3$) before an accelerometer (VEMCO, Halifax, NS. Model V9A-2H, 69 kHz, 16 mm × 67 mm) was gastrically inserted (Cooke et al., 2005). This procedure lasted <2 min and the fish was recovered in the swim tunnel overnight at a water velocity of 0.15 m $s^{-1}$. Each individual completed a standard ramp critical swimming speed ($U_{crit}$) swim protocol (Jain et al., 1997; Lee et al., 2003) at up to six temperatures (12, 14, 16, 18, 20 and 22 °C). Briefly, water velocity was incrementally increased from a resting swim speed of 0.15 m $s^{-1}$ up to 0.65 m $s^{-1}$ (~50% of $U_{crit}$) over a 15-min period. Thereafter, the water velocity was increased by 0.15 m $s^{-1}$ (~0.20 BL $s^{-1}$) every 20 min until the fish ceased swimming and remained on the rear grid for >10 s. Once a fish had fatigued, water velocity was decreased to 0.15 m $s^{-1}$ and the individual was allowed to recover for 1 h following the trial, before temperatures were changed. Temperature was increased or decreased by no more than 4 °C $h^{-1}$ (Clark et al., 2008). Once at the required temperature, individuals were allowed 1 h to equilibrate before the next swim trial began. Two swim trials were completed each day, each at a randomly selected temperature (12, 14, 16, 18, 20 or 22 °C). Once an individual fish was placed in the tunnel, they were allowed to swim at 4 or 6 water temperatures over a period of 2 or 3 days, recovering overnight at the rest swimming speed of 0.15 m $s^{-1}$. In total, 10 individuals (4 females and 6 males) tagged with an accelerometer and 7 control, non-tagged individuals (4 males and 3 females) were tested. One tagged female was excluded from analyses because it refused to swim.

### 2.3. Acceleration and $MO_2$ data collection

Oxygen consumption ($MO_2$) was measured using a dissolved oxygen probe (Mark IV Oxyguard probe; Point Four Systems, Richmond, BC, Canada), Windaq box (Dataq Instruments, Akron, ON, USA) and

Labview software (National Instruments, TX, USA), and was calculated from the decrease in dissolved oxygen during the last ~10 min of each water velocity increment and standardized by body mass (Lee et al., 2003). Dissolved oxygen concentration was maintained above 70% saturation throughout the entire trial. Blank runs (without fish) were completed before and after experimental trials had been run to check probe drift and microbial $O_2$ uptake, both of which were negligible. A portable acoustic hydrophone was inserted into the top of the swim tunnel and the receiver unit (VR100; VEMCO, Halifax, NS, Canada) recorded acceleration data throughout each swim trial. Accelerometers measured acceleration in three axes, for 10 s with a sampling frequency of 10 Hz. The root mean square (RMS) acceleration was calculated by averaging acceleration in all three dimensions using equation; $RMS = (X^2 + Y^2 + Z^2)^{0.5}$, transmitted every 13–17 s and had a range of 0–4.901 m $s^{-2}$. Swim trials were recorded using one wide-angle, black and white video camera (Panasonic WV-BP312; 4.5 mm focal length) in aluminum casing, connected to a time-lapse VCR (Panasonic AG-6124, Panasonic, Secaucus, NJ, USA) to allow for later quantification of TBF. $U_{crit}$ was calculated according to Beamish (1978).

Tailbeat frequency was determined during the first 5 min of each $MO_2$ measurement from the 14 °C swim trial by counting tailbeats during the 10-s period that corresponded with the 10-s sampling period for the accelerometer (~15 10-s period per speed increment). Swim speed was corrected for blocking effect (Jones et al., 1974), and compared to mean acceleration during the last 10 min of each swim speed increment. $MO_2$ was compared with the mean acceleration during the $MO_2$ sampling period.

### 2.4. Field assessment of acceleration transmitter performance

Sockeye salmon for field assessments were caught by rod and reel angling using a charter vessel in the Fraser River estuary throughout September 2011 ($n = 5$; water temperature = 10–13 °C). Fish were placed in a foam-lined trough filled with water, and an acceleration transmitter (VEMCO, Halifax, NS. Model V9AP-2H, 69 kHz, 16 mm × 67 mm) equipped with a pressure sensor was inserted into the stomach via gastric insertion, as in the laboratory experiment. Unlike the laboratory experiment, an anesthetic was not used in an effort to decrease handling time and minimize behavioral changes. The accelerometer sampling time period was the same as the V9A tags used in the laboratory experiment (mean acceleration in three axes over 10 s, at rate of 10 Hz). The V9AP tags transmitted every 13–17 s, alternating between acceleration and depth (m). A blood sample was taken via caudal venipuncture using a vacutainer tube (4 mL, sodium–heparin anticoagulant, BD, NJ; 21 G, 11/2′ long syringe; BD, NJ), placed on ice water slurry for <30 min, and centrifuged for 5 min at 800 *g* (Clay Adams Compact II Centrifuge, Becton-Dickson; Sparks, MD, USA). Erythrocytes and plasma were separated and flash frozen in liquid nitrogen and stored at −80 °C until analysis. Sex was later determined by comparing plasma testosterone and 17β-estradiol which were determined using radioimmunoassay (McMaster et al., 1992). Fork length of fish was measured, and a tissue (<0.1 g) sample from the adipose fin was collected for population identification (Beacham et al., 1995, 2004). Fish were immediately released, and manually tracked for up to 1 h using VR100 portable acoustic hydrophone and receiver unit. Cost of transport (COT) was calculated according to Lee et al. (2003) where COT is a measure of the amount of energy used in relation to the distance traveled.

### 2.5. Statistics

Statistical analyses were completed using RStudio (v. 0.94.110). Data were tested for normality and homoscedasticity. Data failing homoscedasticity was square root transformed. Linear mixed model was used to describe the relationship between TBF and acceleration, as well as the relationship between swim speed and acceleration, and $MO_2$ and acceleration, using temperature, sex, and FL as covariables where applicable and with subject ID as a random factor (to account for non-independence of data). The most parsimonious models were chosen based on second-order information criterion (AICc) (Sugiura, 1978). Mixed model regressions were run with a group of fish implanted with the same acceleration transmitter. Two regressions were completed using six fish implanted with unique tag ID's, a full model, incorporating random slope and random intercept, was compared to a reduced model, which held only intercept as random using AICc. Comparisons between tagged and non-tagged individuals were made using student t-test, with treatment (tagged/non-tagged) as categorical predictor variable. Significance levels for all tests were $p < 0.05$.

## 3. Results

Sockeye salmon maintained steady-state swimming at water velocities between 1 BL $s^{-1}$ and 1.75 BL $s^{-1}$. Below 1 BL $s^{-1}$ tailbeats were irregular while at swim speeds exceeding 1.75 BL $s^{-1}$ fish exhibited "burst and coast" behavior whereby fish would burst to the front of the tunnel and fall back to the back of the swim tunnel. Maximum $MO_2$ of tagged individuals at 14 °C ($9.92 \pm 0.42$ mg $O_2$ $kg^{-1}$ $min^{-1}$) was not significantly different ($t = 0.675$, d.f. = 13, $p = 0.523$) compared with non-tagged individuals ($9.50 \pm 0.52$ mg $O_2$ $kg^{-1}$ $min^{-1}$). The same was true for $U_{crit}$ at 14 °C (tagged = $1.75 \pm 0.07$ BL $s^{-1}$, $1.32 \pm 0.07$ m $s^{-1}$ and non-tagged = $1.66 \pm 0.09$ BL $s^{-1}$, $1.22 \pm 0.09$ m $s^{-1}$; $t = 0.783$, d.f. = 13, $p = 0.448$). $MO_2$ did not differ significantly between tagged males ($10.27 \pm 0.43$ mg $O_2$ $kg^{-1}$ $min^{-1}$) and tagged females ($9.23 \pm 0.61$ mg $O_2$ $kg^{-1}$ $min^{-1}$) ($t = -1.371$, d.f. = 7, $p = 0.213$). The same was true for $U_{crit}$ (males = $1.71 \pm 0.10$ BL $s^{-1}$, $1.37 \pm 0.07$ m $s^{-1}$ and females = $1.81 \pm 0.15$ BL $s^{-1}$, $1.24 \pm 0.10$ m $s^{-1}$; $t = 0.583$, d.f. = 7, $p = 0.578$).

### 3.1. Tailbeat frequency, swim speed and $MO_2$

The relationship between acceleration and TBF for each of the nine fish was determined at 14 °C (Fig. 1, left column). There was a significant positive linear relationship between acceleration and TBF for all individuals, with an overall $R^2$ of 0.81 (range 0.55 to 0.87; Table 1). Of the nine fish tested, six fish were implanted with unique tag IDs (see Fig. 2B). Two regressions were completed using these six fish, the full model, incorporating random slope and random intercept was compared to the reduced model, incorporating only slope. The reduced model was a better fit ($\Delta AICc = 0$) than the full model ($\Delta AICc = 2.08$). Three fish were implanted with the same tag (see Fig. 2A). The relationship between acceleration and TBF for all nine fish was determined using the reduced mixed model, where the model with the best fit included sex and TBF as predictor variables and fish ID was held as a random variable. There was a significant interaction between TBF and sex ($p = 0.002$; Table 2), whereby TBF was lower for males.

Acceleration values varied with swimming speed (Fig. 1; center column). The model of swim speed and acceleration was determined using a mixed model, with FL and acceleration as predictor variables and fish ID held as the random variable. Acceleration ($p < 0.0001$) had positive effects on swim speed whereas fork length ($p = 0.051$) had a negative effect on swim speed (Table 2).

$MO_2$ of each fish increased with increasing acceleration values (Fig. 1; right column, Fig. 3). The relationship between $MO_2$ (mg $O_2$ $kg^{-1}$ $min^{-1}$) and acceleration (m $s^{-2}$) was developed using mixed model, where FL, temperature, sex, and acceleration were predictor variables and fish ID was held as a random factor. Acceleration ($p < 0.0001$) and temperature ($p < 0.0001$) were the only significant

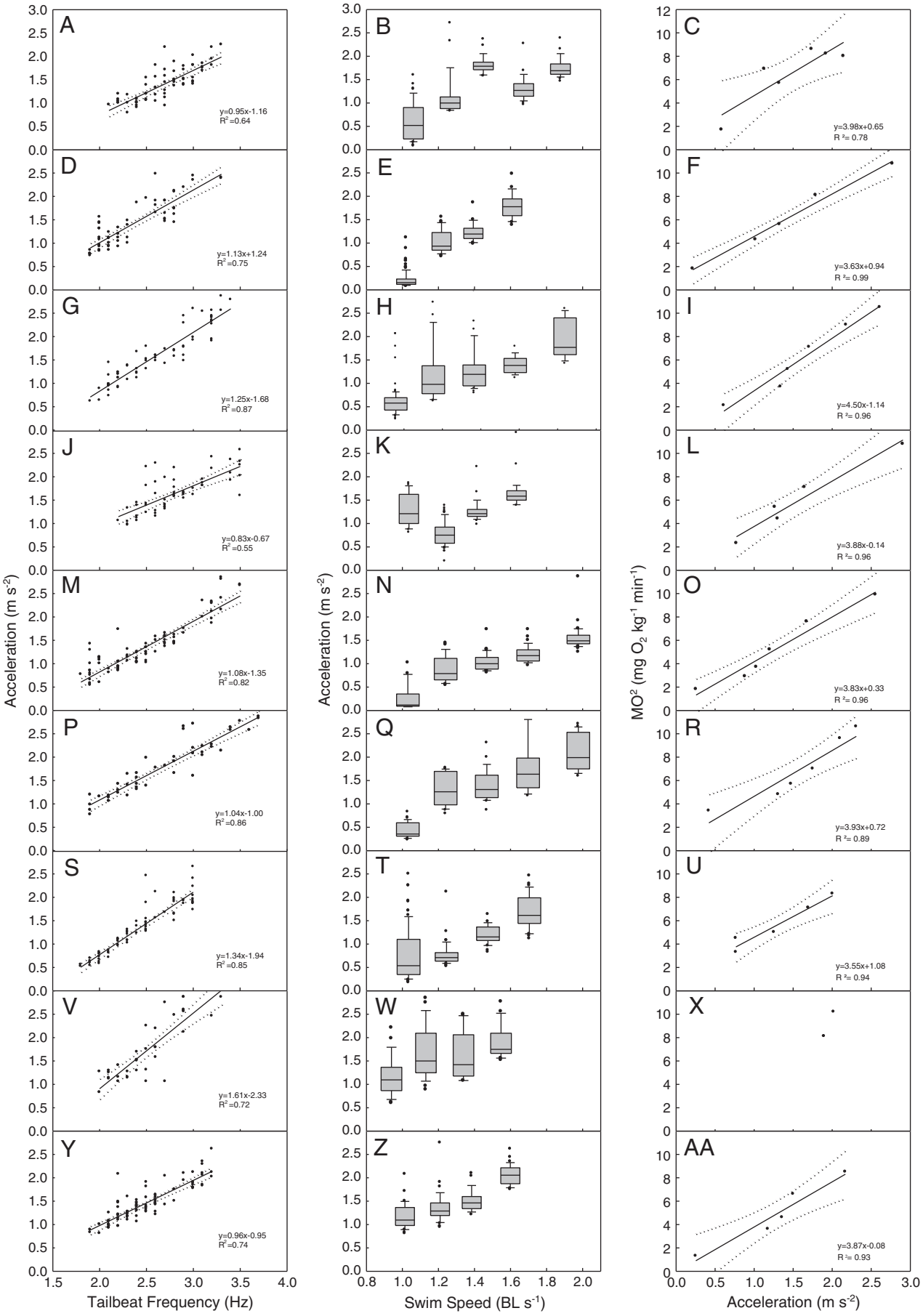
A
y=0.95x-1.16
R²=0.64
B
C
y=3.98x+0.65
R ²= 0.78
D
y=1.13x+1.24
R²=0.75
E
F
y=3.63x+0.94
R ²= 0.99
G
y=1.25x-1.68
R²=0.87
H
I
y=4.50x-1.14
R ²= 0.96
J
y=0.83x-0.67
R²=0.55
K
L
y=3.88x-0.14
R ²= 0.96
M
y=1.08x-1.35
R²=0.82
N
O
y=3.83x+0.33
R ²= 0.96
P
y=1.04x-1.00
R²=0.86
Q
R
y=3.93x+0.72
R ²= 0.89
S
y=1.34x-1.94
R²=0.85
T
U
y=3.55x+1.08
R ²= 0.94
V
y=1.61x-2.33
R²=0.72
W
X
Y
y=0.96x-0.95
R²=0.74
Z
AA
y=3.87x-0.08
R ²= 0.93
Acceleration (m s-2)
Acceleration (m s-2)
MO2 (mg O2 kg-1 min-1)
Tailbeat Frequency (Hz)
Swim Speed (BL s-1)
Acceleration (m s-2)

**Table 1**
Linear regressions for TBF and acceleration at 14 °C for each of the nine fish tagged with acceleration transmitters.

| Fish ID | Sex | FL (cm) | Tag ID | m | b | $R^2$ |
|---|---|---|---|---|---|---|
| 3F07 | M | 63.4 | 21 | 1.08 | −1.35 | 0.82 |
| 1759 | F | 60.5 | 22 | 0.95 | −1.16 | 0.64 |
| 4 F25 | F | 61.2 | 24 | 1.04 | −1.00 | 0.86 |
| 3645 | M | 63.5 | 25 | 1.13 | 1.24 | 0.75 |
| 1E09 | M | 64.3 | 23 | 0.83 | −0.67 | 0.55 |
| 6849 | M | 67.2 | 21 | 1.26 | −1.68 | 0.87 |
| 557E | M | 60.0 | 26 | 1.34 | −1.94 | 0.85 |
| 7F2F | F | 64.5 | 23 | 0.96 | −0.95 | 0.74 |
| 6B2C | M | 68.9 | 26 | 1.61 | −2.33 | 0.72 |

m = slope, b = y-intercept of the linear regression between TBF and acceleration.

predictor variables, both having positive effects on $MO_2$. FL and sex were non-significant ($p > 0.05$; Table 2; Fig. 3).

$$MO_2 = 0.22(\text{Temperature } (^\circ\text{C})) + \begin{pmatrix} 0.61 & \text{Male} \\ 0 & \text{Female} \end{pmatrix} - 0.05(\text{FL}) + 4.39(\text{Acceleration}) - 0.12 \quad (1)$$

### 3.2. Field assessment

Of the five fish tagged (three males, two females) with acceleration transmitters, three fish (one male, two females; all Harrison River population) were tracked for up to 1 h after release, but two fish (two males; one Harrison River and one Weaver Creek population) immediately traveled outside of the detection radius of the manually tracking area so no acceleration values were recorded. Acceleration values from three tracked fish ranged from 0.538 to 2.845 m $s^{-2}$, which are within the range of acceleration values observed in controlled swim trials (see Fig. 4). Mean (±SE) swimming speed was estimated as 1.25 ± 0.03 BL $s^{-1}$ and mean $MO_2$ as 3.39 ± 0.17 mg $O_2$ $kg^{-1}$ $min^{-1}$ using the swim speed–acceleration and acceleration–$MO_2$ models (Eq. (1)) for 11.0 °C. Mean COT of adult sockeye salmon swimming in the Fraser River estuary was 0.070 ± 0.002 mg $O_2$ $kg^{-1}$ $m^{-1}$.

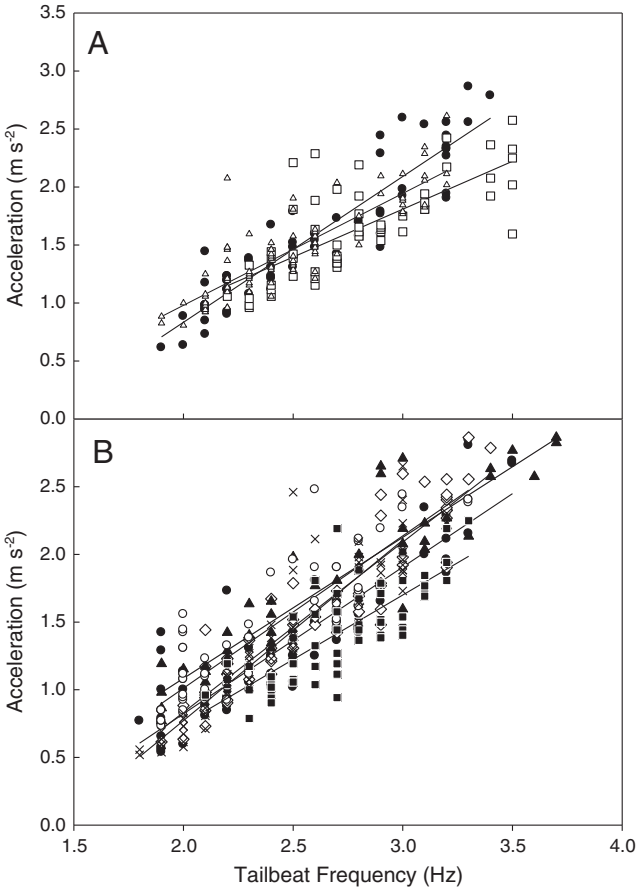


**Fig. 2.** The relationship between TBF and acceleration at 14 °C for A) three adult sockeye tagged with the same V9A-2H acceleration transmitter and B) six individual adult sockeye salmon gastric tagged with six unique V9A-2H acceleration transmitters. Each line represents the relationship between TBF and acceleration for a single fish. Each symbol represents an individual sockeye salmon. (Open symbols = females; closed symbols = males).

## 4. Discussion

Despite being the best studied of the Pacific salmons (Hinch et al., 2006), little is known about energy use of returning adult sockeye salmon throughout their marine migration. The few studies that directly examined energy use using activity transmitters (EMG) were limited to freshwater assessments in short segments of sockeye salmon's river migration, and had relatively small sample sizes (Hinch and Rand, 1998; Rand and Hinch, 1998; Hinch et al., 2004). The development of acoustic acceleration transmitters has enabled the remote observation of fine-scale activity and energy use patterns in both the marine and freshwater sections of spawning migration. However, use of such tags for field-based studies of energetics is predicated on the calibration of transmitter output with $MO_2$ and swimming speed. This study was the first validation of acoustic transmitter-accelerometers to estimate energy expenditure in a free-swimming vertebrate, thus supporting the use of this technique for monitoring tagged animals released into the wild.

Accelerometer loggers operating at a higher sampling frequency and for continuous periods compared with transmitters have been shown to accurately reflect swimming movement patterns in fish (Shepard et al., 2008; Gleiss et al., 2010). Nevertheless, the strong linear correlations between TBF and acceleration for each individual in the current study ($0.55 > R^2 < 0.87$; mean = 0.81) at acceleration values <3 m $s^{-2}$, clearly shows that a much lower sampling frequency (10 Hz) and sampling period (10 s) are adequate for estimation of $MO_2$ in adult migrating sockeye salmon. Previously, accelerometer loggers used in aquatic organisms provided a correlation coefficient between acceleration and movement of around 0.7, as found in the present study, which is lower than the 0.9 correlation coefficient typical of terrestrial organisms (Halsey et al., 2009; Gleiss et al., 2010). Above a TBF of 2.5 Hz, fish began to exhibit bursting behavior, resulting in higher acceleration values and weakening the correlation between TBF and acceleration. Accelerations beyond 3.0 m $s^{-2}$ failed to follow any relationship and were excluded from this study. Acceleration varied only slightly at a given swim speed, indicating that the accelerometer output successfully integrated aspects of locomotion beyond TBF that contribute to swimming speed, such as tailbeat amplitude and other fine-scale differences in locomotion. It is unclear from the present experiments why high accelerations were not correlated with swimming speed. Future studies could examine both TBF and tailbeat amplitude to resolve this problem. Nevertheless, TBF and acceleration provided a strong correlation that proved useful for examining fish swimming in a natural setting.

Sockeye salmon used here had naturally ceased feeding as part of their spawning migration and could be tagged via gastric insertion. Thus, handling time under anesthesia was greatly reduced compared

**Fig. 1.** Relationships between acceleration and TBF (left column), acceleration and swim speed (center column), and $MO_2$ and acceleration (= m $s^2$; right column) for individual sockeye salmon at 14 °C. Each row represents relationships for a single fish. Dotted lines represent 95% confidence intervals.

**Table 2**
Significance of variables and variable interactions for acceleration and TBF, acceleration and swim speed and $MO_2$ and acceleration relationships for the nine fish tagged for the laboratory study.

| | |
|---|---|
| Acceleration & tailbeat frequency | p value |
| Sex | 0.0769 |
| TBF | <0.0001 |
| TBF∗sex | 0.0020 |
| Swim speed & Acceleration | p value |
| FL | 0.0508 |
| Acceleration | <0.0001 |
| $MO_2$ & acceleration | p value |
| Acceleration | <0.0001 |
| FL | 0.1567 |
| Sex | 0.0627 |
| Temperature | <0.0001 |

with EMG and ECG tagging, which require surgical implantation. Whereas positioning and securing of EMG and ECG tags are under precise control, exact orientation and position cannot be controlled during gastric insertion. To determine if potential tag placement differences altered the individual relationships between TBF and acceleration, a full mixed model was compared with a reduced mixed model (Brown et al., 2007). The reduced model was a better fit, suggesting that the calibration relationships were not dependent on exact tag placement and could be applied to other non-calibrated sockeye salmon in nature. The regressions for six fish tagged with unique tag IDs did not differ, and likewise the regressions for three individuals tagged with the same tag ID were not different. Data from each fish were grouped to determine a single relationship between TBF and acceleration. This demonstrated that the acceleration transmitters, sampling at a rate of 10 Hz for 10 s, accurately reflected swimming activity of adult sockeye salmon, independent of precise gastric placement and orientation.

Ambient water temperature is the driving factor of basal metabolic rate in fish (Fry, 1971; Brett, 1995). Previous studies have shown that individual adult sockeye salmon experience water temperatures ranging between 8 and 21 °C during their upriver spawning migration (Patterson et al., 2007). As a result they have population specific differences in thermal tolerance, and aerobic scope (Eliason et al., 2011). In this study we examined both basal and active metabolic rate in fish over a thermal range (12–22 °C), which incorporates both typical temperatures experienced by migrating sockeye salmon, as well as an extreme temperature (22 °C) that is rarely experienced by migrating adult sockeye salmon, and considered to be at the limit

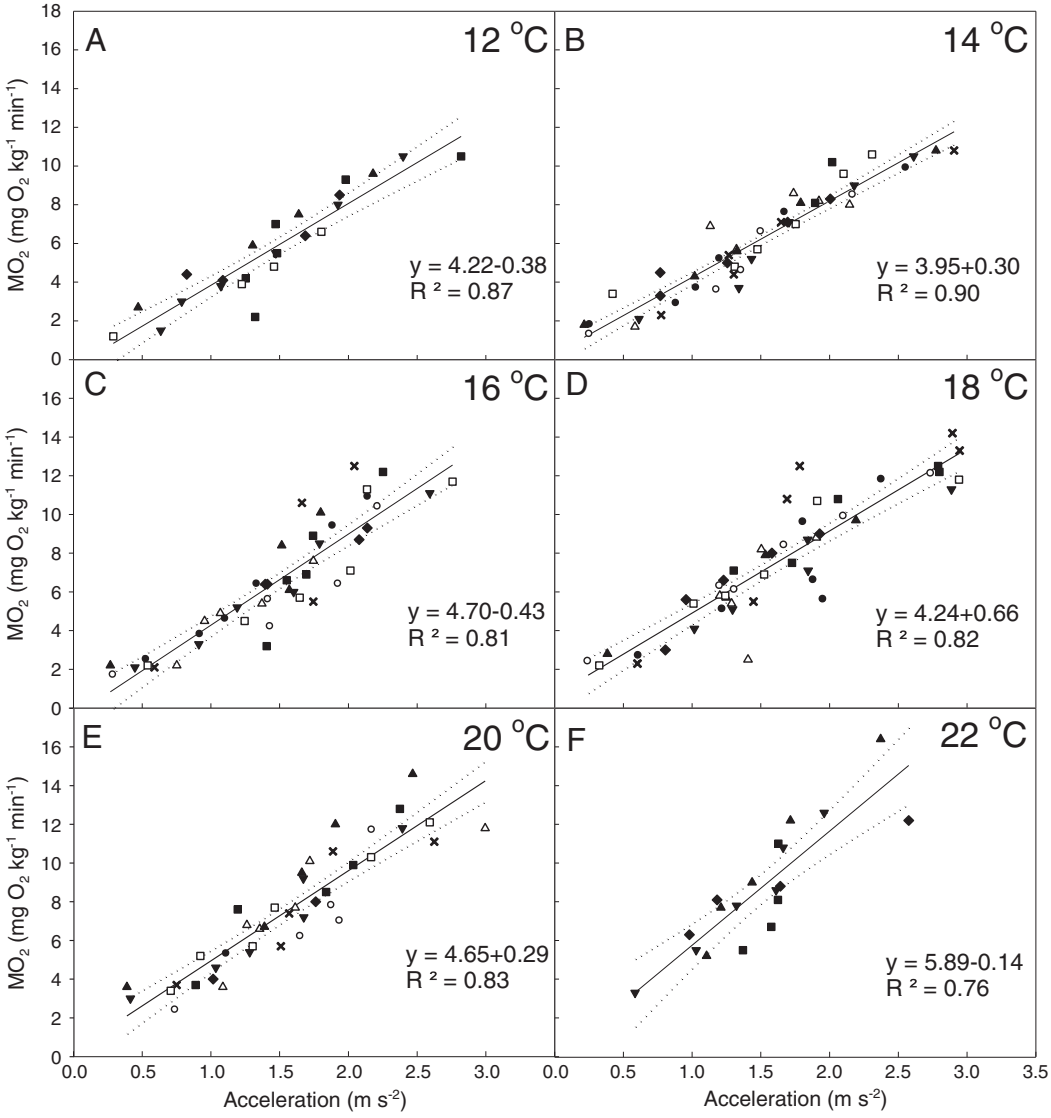


**Fig. 3.** Relationship between $MO_2$ and acceleration at A) 12 °C, B) 14 °C, C) 16 °C, D) 18 °C, E) 20 °C and F) 22 °C. Each line represents the relationship between $MO_2$ and acceleration for all fish swam at a given temperature. Each symbol represents and individual sockeye salmon. (Open symbols = females; closed symbols = males).

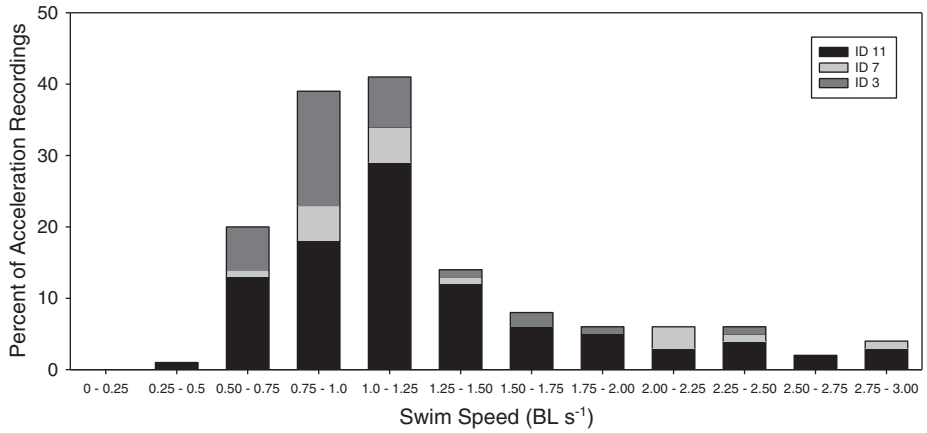


**Fig. 4.** Percent of detections at a swim speeds for three sockeye salmon released in the Fraser River estuary. Tag ID used to identify the proportion of detections from a given fish at each swim speed. Swim speeds determined using relationship between acceleration and swim speed.

of thermal tolerance (Eliason et al., 2011). Sockeye salmon can experience highly variable water temperatures within a short period of time (Patterson et al., 2007) and can withstand the change of 4 °C $h^{-1}$ used in this experiment (Clark et al., 2008). Although adult Harrison River sockeye salmon have a very shallow and broad aerobic scope (Eliason et al., submitted for publication), temperature was found to be a significant predictor of oxygen consumption (Eq. (1)), and was included in the model.

Movement is correlated to energy use in migrating sockeye salmon (Brett, 1965). Correspondingly, the acceleration transmitters relayed information that provided a strong relationship between acceleration and $MO_2$. Linear regressions of all fish grouped together for each temperature indicated a strong correlation between $MO_2$ and acceleration. The model of best fit revealed that $MO_2$ was positively related to both acceleration and temperature. These findings are consistent with previous work showing that $MO_2$ in sockeye salmon varies with swim speed and temperature (Brett, 1965; Eliason et al., 2011). Moreover, the model of $MO_2$ and acceleration can be used to generate empirically validated estimates of energy use by migrating adult sockeye salmon using acoustic accelerometers.

The final objective of this study was to conduct a field-based proof-of-principle validation of the acoustic acceleration transmitters. Manual tracking revealed accelerations well within the calibrated range for both TBF and $MO_2$, obviating any problem associated with high accelerations. It is possible that tagged and released sockeye salmon were physiologically exhausted and thus exhibited decreased activity compared to unhandled fish. Future studies should interpret acceleration values that fall outside of the calibrated range cautiously. The relatively low power output of V9 tags made manual tracking a challenge since two fish quickly escaped the receiver detection radius. Acceleration transmitters with a higher power output (i.e. VEMCO V13 tags with higher dB) are now available, which increases detection radius and may facilitate both manual tracking efforts and increase detection efficiency of stationary acoustic receivers.

Although this study demonstrated that acceleration transmitters can relay information on swimming speed and estimate energy use in nature, the ecological relevance of these values must be evaluated. The estimate of average swim speed (~1.3 BL $s^{-1}$) is very similar to optimal speed (~1 BL $s^{-1}$) reported elsewhere for marine migrating adult Pacific salmon (reviewed in Drenner et al., 2012), and so appears realistic. Using respirometry, Wagner et al. (2006) found that sockeye salmon swimming at speeds close to 1.25 BL $s^{-1}$ consumed ~11.0 mg $O_2$ $kg^{-1}$ $min^{-1}$ at 12.5 °C in freshwater, whereas Brett (1965) found that $MO_2$ was 2.93 mg $O_2$ $kg^{-1}$ $min^{-1}$ at 15 °C. In this study, $MO_2$ for three tracked fish was estimated as ~3.4 mg $O_2$ $kg^{-1}$ $min^{-1}$ using laboratory derived calibrations. However, Wagner et al. (2006) found a 27% higher $MO_2$ for sockeye salmon swimming at ~1.25 BL $s^{-1}$ in seawater compared with freshwater. Since the laboratory calibrations were performed in freshwater, and study fish were swimming in seawater, a correction for 27% should be applied, which yields an average $MO_2$ of 4.3 mg $O_2$ $kg^{-1}$ $min^{-1}$, and is still well within the range of observed rates of $MO_2$ in seawater (~4.0 to 15.0 mg $O_2$ $kg^{-1}$ $min^{-1}$, at 12.5 °C; Wagner et al., 2006). Nevertheless, the energetic cost of swimming in seawater needs to be confirmed in seawater laboratory studies over a range of temperatures to ensure accuracy of field-based estimates of metabolic rates.

To date, few studies have directly measured adult sockeye salmon $MO_2$ to estimate COT under laboratory conditions (e.g., Brett, 1965; Lee et al., 2003; MacNutt et al., 2006). For example, Lee et al. (2003) found COT varied from ~0.14 mg $O_2$ $kg^{-1}$ $m^{-1}$ to 0.21 mg $O_2$ $kg^{-1}$ $m^{-1}$ at 1.25 BL $s^{-1}$ at 12 °C. Wagner et al. (2006) found that at the same water temperature and swim speed COT was ~0.12 mg O2 /kg/m in freshwater and ~0.17 mg $O_2$ $kg^{-1}$ $m^{-1}$ in seawater. Only one study has estimated COT in the field, which was 0.14 mg $O_2$ $kg^{-1}$ $m^{-1}$ at 18 °C for free-swimming adult sockeye salmon in a non-constricted reach of the Fraser River (Hinch and Rand, 1998). Using laboratory derived calibrations, we estimated COT to be ~0.07 mg $O_2$ $kg^{-1}$ $m^{-1}$ for fish swimming in freshwater and ~0.09 mg $O_2$ $kg^{-1}$ $m^{-1}$ for fish swimming in saltwater in the Fraser River estuary. Temperature differences among studies could contribute to some but not all of slight differences in COT among studies, since Lee et al. (2003) showed a clear positive relationship between COT and temperature. Overall, it was determined that both rate of $MO_2$ and COT estimated using acceleration transmitters, were ecologically realistic as they fell close to previously observed values.

## 5. Conclusions

In conclusion, this study verified that the acceleration information from VEMCO V9A transmitters can be used as a proxy for swimming speed in laboratory trials, and that laboratory-derived calibrations can be used to estimate COT in free-swimming fish in a natural environment. The above estimates of average swimming speed and COT in nature were well within the previously observed range derived in laboratory studies. Thus, VEMCO acceleration transmitters are a promising new tool for advancing our understanding of the activity patterns and energetics of fish in the wild.

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