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**Energetic costs of activity in wild Lake Trout: a calibration study using
acceleration transmitters and positional telemetry**

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Abstract

Acceleration telemetry transmitters offer the opportunity to estimate the cost of behaviours in free-ranging fish, but a methodology to translate acceleration data into metabolic equivalents is still needed. This study extends previous calibration studies, explores how well tail-beat frequency transmitters fulfill their role, and presents a procedure to convert acceleration data into metabolic cost within a framework consistent with traditional fish bioenergetics models and thus facilitates comparisons of energetic costs between natural fish populations. These objectives were achieved by comparing data from Lake Trout in a laboratory setting with data from three natural populations. In the laboratory, tail-beat frequency, acceleration values, and oxygen consumption increased progressively with swimming speed. In the wild, individual swimming speeds estimated from positional telemetry were consistently underestimated by, but positively related to, transmitter-based acceleration values. The proposed rationale to estimate metabolic rate from acceleration data accounts for variation in fish weight and environmental temperature. We demonstrated how this novel method permits comparison of metabolic costs associated with the levels of activity typical of Lake Trout living in two different lakes.

Keywords: acceleration, activity, bioenergetics, calibration, Lake Trout, oxygen consumption, swimming speed, telemetry

29 Introduction

30 The study of animal movements is critical to understanding various ecological processes
31 (Nathan *et al.* 2008). Individuals move in response to the environment - abiotic and biotic- and as
32 a result of behaviours that maximize fitness and minimize costs (Bolnick *et al.* 2003; Andersen *et*
33 *al.* 2006). Costs are frequently expressed in terms of energy budgets that estimate intake and
34 output rates (Kitchell 1983). Energy expenditure in any organism is related to its metabolic
35 activities, with movement constituting a major portion of an energy budget, especially in aquatic
36 organisms (Boisclair and Leggett 1989; Jobling 1994; Fish 2010). The study of aquatic animal
37 movements and bioenergetics has been greatly advanced by the use of telemetry techniques;
38 however, it is still difficult to quantify activity, especially for free-ranging aquatic organisms.
39 Similarly, the application of acceleration technology to bioenergetics studies of free-ranging fish
40 needs a clear methodological framework.

41 Initially, the study of movements linked to energetics was made possible by the use of
42 radio electromyogram and heart rate telemetry techniques (Cooke *et al.* 2004). Later, the
43 development of loggers able to measure acceleration allowed the study of activity in relation to
44 metabolic demands (Wilson *et al.* 2006; Shepard *et al.* 2008; Gleiss *et al.* 2011). These loggers
45 are usually externally implanted, sample acceleration of the whole body of the fish along each of
46 three orthogonal body axes (*i.e.* dorso-ventral, lateral and anterior-posterior, Gleiss *et al.* 2010),
47 and report the sum of these three components of acceleration. This sum is strongly correlated
48 with the energy expended by the organism on activity (Wilson *et al.* 2006; Halsey *et al.* 2009).
49 Recently, the development of small acoustic transmitters with similar three-axial acceleration
50 sampling capabilities has permitted internal implantation into fish and other aquatic biota. This
51 approach has been shown to provide good estimates of activity costs of aquatic organisms

(Murchie *et al.* 2011; Wilson *et al.* 2013). For example, Wilson *et al.* (2013) provided empirical evidence of the direct associations linking tail-beat frequency (TBF), swimming speed (SS) and oxygen consumption in laboratory-held Sockeye Salmon (*Oncorhynchus nerka*). They went on to use these relationships to study the cost of transport for the species in the wild.

A related method of estimating energy expenditure in fish focuses on measuring the TBF. With an increase in SS, the frequency of tail beats increases (Bainbridge 1958) and fish consume more oxygen (Brett 1964). A number of studies have shown that externally fitted transmitters used to record TBF can be used to estimate SS (Kawabe *et al.* 2003) and energy expenditure in free-swimming fish (Lowe *et al.* 1998; Lowe 2002). However, one problem with this technique is the potential impact on swimming performance of the increased hydrodynamic drag caused by the externally fitted transmitter (Mellas and Haynes 1985). A variation of the previously mentioned small acoustic transmitter reports acceleration along the two body axes (dorso-ventral and lateral) that are most cleanly linked to the undulating movements made by the tail when the fish is swimming. This transmitter can be internally implanted and has been shown to be effective at measuring TBF (Dale Webber, VEMCO, Nova Scotia, Canada, personal communication, 2009) and estimating metabolic rates in wild aquatic animals (Payne *et al.* 2011). This technological advance opens new possibilities for the quantification of fish activity and bioenergetics in the field. However, details on the implantation, calibration and use of these TBF transmitters are lacking in the current literature.

This study extends previous calibration studies (Payne *et al.* 2011; Wilson *et al.* 2013) and presents new information on the use of TBF transmitters in a common freshwater salmonid, (Lake Trout, *Salvelinus namaycush*). Specifically, we (i) present laboratory-derived data illustrating the relationships linking SS of tagged Lake Trout to transmitter-acceleration, TBF,

and oxygen consumption; (ii) explore how the transmitter's placement inside the body cavity affects the SS-acceleration relationship; (iii) propose how these relationships may be used to quantify metabolic costs in free-ranging fish in a way that is directly compatible with traditional fish bioenergetics models (eg. Kitchell *et al* 1977) and (iv) present an example illustrating how this method permits informative comparisons of the metabolic costs exhibited by Lake Trout living in two different natural environments.

Materials and Methods

Acoustic transmitters, study fish, and surgical procedures

We used V9-family (VEMCO, Nova Scotia, Canada) acoustic transmitters (9 mm diameter, 46 mm long, 3.3 g in water) throughout this study. Two types of transmitters were used: one measured acceleration only (V9A) and the other measured acceleration and depth (V9AP). Both types of transmitter were designed to focus on capturing just the acceleration of the tail when it is engaged in the lateral, undulating movements that are associated with swimming. Therefore they both measured acceleration along just two axes (dorso-ventral and lateral) and reported their sum, averaged over a specified sampling interval, which in this study ranged from 17 to 45 s (see Table 1). The sampling interval was followed by a user-defined random delay and then the transmitter broadcasted the magnitude of the acceleration at 69 kHz. For V9A transmitters, this acceleration report is followed by another delay and then the next acceleration-sampling interval is initiated. For V9AP transmitters, an instantaneous fish depth (based on pressure, accurate to ± 1.5 m) is reported and immediately after, an acceleration-sampling period is initiated; this period is followed by another random delay and then the average acceleration value is reported. The acceleration-sensor reports values (ranging from 0 to

255) in arbitrary units that are linearly related to the root mean square acceleration (in $\text{m}\cdot\text{s}^{-2}$) experienced by the transmitter in the two directions perpendicular to the anterior-posterior axis of the fish. Therefore, transmitters did not provide a direct measure of the forward acceleration of the fish; instead, they were designed to capture the varying levels of acceleration exhibited by the tail at different values of TBF. In this paper we present all acceleration values in the arbitrary units (a.u.) directly reported by each transmitter.

Given the characteristics of our study (laboratory versus field comparisons of SS and acceleration relationships) and the different questions we address, we incorporated various sampling and reporting intervals in the transmitters (Table 1). In the field, long-delay V9AP transmitters (120 s random delay between transmissions, representing the mean reporting interval) were used to record both activity and depth behaviour over a three-month period. The mean reporting interval for each transmitter-sensor (acceleration or depth) was 240 s. The choice of this interval was the result of a trade-off between several competing objectives: (i) transmitter size must be small (<2% of fish body mass, Winter 1996 and Perry *et al.* 2013, being < 1% in our study) to limit stress on the fish; (ii) battery life (and size) must match the planned duration of the study (minimum of 3 months); (iii) location reporting must be frequent enough to provide accurate estimates of travel distance (Rowcliffe *et al.* 2012); and (iv) the location reporting interval must be long enough to minimize simultaneous reporting ('collisions') by multiple transmitters as this will prevent accurate triangulation of location by the receiver network. To evaluate how much variation in movement was missed with the long-delay transmitters, we included one short-delay transmitter (mean reporting interval of 25 s, Table 1) in a separate control lake (Lake 375). In the laboratory, short-delay V9A transmitters (25 s fixed delay, Table 1) were used to maximize the amount of acceleration data obtained before tiring the fish, and

because neither battery life nor depth data were relevant for this part of the study. These short-delay transmitters were supplemented with three long-delay V9AP transmitters (Table 1). The transmitters were reused in the laboratory after fish completed the experimental trials.

In the laboratory, 46 Lake Trout from hatchery stock (mean fork length 494 mm, Table 1) were used: 30 fish were implanted with TBF-transmitters and an additional 16 fish were used to measure oxygen consumption. There were two main reasons for not implanting TBF-transmitters in the laboratory fish used for the oxygen consumption trials. First, implantation represents a trauma to the fish, which requires a healing time that may be longer than the recovery period allowed for it, during which physiological parameters can be affected, and can be reflected in the oxygen consumption. Second, implantation of small (<1 % of fish body weight in our study) internal transmitters does not affect the drag that the fish experience, nor does it affect the morphology or the physical movement of the tail of the fish. Therefore, we did not expect any differences in body movements or oxygen consumption for fish implanted with a TBF-transmitter compared to fish without a transmitter (larger transmitters may represent a burden on fish performance, Perry *et al.* 2013). In the wild, a total of 21 fish (mean fork length 411 mm, Table 1) were angled with barbless hooks and implanted with TBF-transmitters.

Transmitter implantation in the field and in the laboratory followed standard surgical procedures (Mulcahy 2003; Harms 2005; Blanchfield *et al.* 2005) (details in *SI*¹). In summary, fish were anaesthetized, a small mid-ventral incision was performed to insert the transmitter into the body cavity, and sutures closed the incision. In the laboratory, the transmitters were pushed towards the caudal end of the body cavity, until significant resistance was met, to ensure a proper placement of the TBF transmitters (except for fish tested for the effect of transmitter placement, see below). In the field, the transmitters were tethered and sutured to the incision to ‘secure’

¹ Supplementary material is available on a separate document submitted with this manuscript

them in place (Webber, personal communication, 2009). After surgery, fish were placed in an aerated freshwater bath to recover. Upon recovery, wild fish were released to their lake and laboratory fish were moved to individual 267 L holding tanks supplied with aerated freshwater where they were left to further recover from surgery for one week. The use of animals for this study was reviewed and approved by the Animal Care Committee of each institution involved (Department of Fisheries and Oceans, Ontario Ministry of Natural Resources, and University of Toronto).

Laboratory trials

All laboratory experiments were performed at the Codrington Fisheries Research Facility of the Ontario Ministry of Natural Resources, in Codrington, Ontario, Canada. The fish used in these trials were first generation Lake Trout derived from wild spawn collections conducted on Lakes Opeongo and Louisa in Algonquin Provincial Park in 2003 and 2004 (McDermid *et al.* 2010). Prior to being selected for the experiments, these fish were reared in 1059 L circular fiberglass tanks at ambient water temperatures between 5 and 12 °C and fed commercial trout pellets. Because the time spent in the hatchery by these fish was brief (one generation) and the hatchery was a research facility where feeding and treatment conditions were designed to limit directional selection, we felt that it was reasonable to apply the performance data of these laboratory fish to wild individuals in their natural environments.

Laboratory experiments assessed fish swimming performance over a set of controlled replicable levels of activity. This was accomplished using a 156 L swim tunnel (Loligo Systems, Denmark) that provided recirculating water flowing through a holding compartment (dimensions: 70 cm length, 25 cm width, and 24 cm height) where fish were placed (details of

the swim tunnel in *S2* and Fig. *S1*). The rate of water flow was regulated by a frequency converter, which was calibrated ($0.1 \text{ Hz} = 0.35 \text{ cm} \cdot \text{s}^{-1}$) with a flow meter (FP101 & 201, Global Water, California, USA). The final speed in the swim tunnel was corrected, as proposed by Bell and Terhune (1970), for the solid blocking effect because 30 % of the experimental fish occupied more than 10 % of the swim tunnel cross-sectional area. However, the dimensions of the holding compartment allowed for natural swimming by the experimental animals, and they were able to respond to the increments applied over the range of swimming speeds sampled.

Transmitter position within the body cavity

We carried out a set of studies to evaluate: (i) how the sampling of acceleration is affected by transmitter position inside the fish; and (ii) the ‘natural’ movement of a transmitter within the body cavity of a fish. Six fish (Table 1) were selected from the hatchery stock. Three were implanted with transmitters in the mid-ventral portion of the abdomen and a suture to the incision was used to tether the transmitter in place. Three other fish were implanted with two transmitters; one tethered to the incision in the mid-ventral position, the second placed untethered toward the end of the body cavity. The weight of the two transmitters together was less than 1% of the fish body weight and there was sufficient space in the body cavity to accommodate both transmitters. Each fish was then exercised over the same range of swimming speeds and the relationship between SS and transmitter-based acceleration measurement was compared between transmitters within a fish, and among fish. At the end of these exercise experiments, all fish were euthanized; the position of each transmitter within the body cavity was determined and compared with its position when it was first implanted.

Comparison of TBF, SS and transmitter-based acceleration

Twenty-four fish (pooled mean fork length 480 mm, Table 1) were used to characterize the relationship between SS, TBF, and the acceleration values reported by the TBF-transmitter. Exercise trials included a period of habituation to the holding compartment of the swim tunnel followed by a period of actual exercise on each individual fish. The habituation occurred at a flow rate of $13 \text{ cm}\cdot\text{s}^{-1}$ ($1/4$ body lengths per second [$\text{BL}\cdot\text{s}^{-1}$]) for 1 h (Jain *et al.* 1997; Peake *et al.* 1997). For the exercise trial itself, water flow speed was increased at fixed increments of $3.5 \text{ cm}\cdot\text{s}^{-1}$ for a mean duration of 5 min (3 – 7 min) of exposure to each SS, until each individual fish reached fatigue (Kolok 1999). This typically occurred after about 90 min (60 – 120 min) at speeds of up to $80 - 95 \text{ cm}\cdot\text{s}^{-1}$ ($1.5 \text{ BL}\cdot\text{s}^{-1}$ and up). Each fish was exercised on three separate occasions, allowing 24 h in between for recovery. The acceleration values reported by the transmitters implanted in fish were recorded using a receiver-logger (VR100, VEMCO, Nova Scotia, Canada). Swimming behaviour during each trial was recorded using a video recorder (Panasonic SDR-H85) looking down vertically on the fish in the holding compartment of the swim tunnel. Video recordings were analyzed visually to obtain estimates of mean TBF (counts of full lateral beats, from side to side of the fish, per minute) for each tagged fish swimming at SS of 0.5, 1, and $1.5 \text{ BL}\cdot\text{s}^{-1}$ (details in S3).

Oxygen consumption versus SS

To characterize the relationship between Lake Trout oxygen consumption and SS, we recorded the respiration rate of individual fish ($n=16$, mean fork length 507 mm, Table 1) at each of three swimming speeds: $30 \text{ cm}\cdot\text{s}^{-1}$ ($\sim 0.5 \text{ BL}\cdot\text{s}^{-1}$), $57 \text{ cm}\cdot\text{s}^{-1}$ ($\sim 1 \text{ BL}\cdot\text{s}^{-1}$), and $83 \text{ cm}\cdot\text{s}^{-1}$ ($\sim 1.5 \text{ BL}\cdot\text{s}^{-1}$) at ambient water temperatures ($11.76 \pm 1.26 \text{ }^{\circ}\text{C}$). For one month prior to the experiments,

all fish were acclimated in 267 L semi-square tanks (Hammer 1995) and fed to satiation. Twenty-four hours before an experiment, each trial fish was fasted to ensure that it was in a proper post-absorptive state. It was then transferred to the swim tunnel and permitted to habituate at a fixed SS of $13.5 \text{ cm} \cdot \text{s}^{-1}$ ($1/4 \text{ BL} \cdot \text{s}^{-1}$) for 1 h. After acclimation, the speed of the water through the tunnel was increased gradually until the desired speed was reached; thereafter, the fish was forced to swim at that fixed speed for 1 h or until it reached fatigue. During each experiment, we ensured that the oxygen saturation of the water remained $>70\%$, so that recorded respiration would be independent of oxygen saturation (Beamish 1964). The concentration of dissolved oxygen (DO_2) in water was measured during the experiment (YSI ProODO, YSI Incorporated, Yellow Springs, Ohio, USA). After the exercise period, the fish was removed from the swim tunnel and allowed to recover in one of the semi-square tanks. Experimental runs without fish were done before and after each trial to estimate the variations in oxygen concentration due to microbial consumption in the tunnel and/or probe accuracy and it was insignificant. The rate of oxygen consumption (MO_2) per gram of fish weight was calculated using the formula:

$$\text{MO}_2 = \frac{(\text{DO}_{2b} - \text{DO}_{2e}) \cdot (\text{tank volume} - \text{fish volume})}{(\text{fish weight}) \cdot (\text{time})}$$

where $\text{DO}_{2b,e}$ refer to the DO_2 ($\text{mg O}_2 \cdot \text{L}^{-1}$) at the beginning and end of the exercise period (time in h), and the volume (L) of the fish is estimated by assuming 1 L of volume per kg of fish weight (Farrell *et al.* 2003). Respiration rate values were compared with previous studies, summarized for Lake Trout in Evans (2007), by using our results to estimate the respiration rate for a 100 g fish using an allometric weight power coefficient of 0.85 (Beamish *et al.* 1989).

Field Trials

Field tracking of Lake Trout and assessment of acceleration transmitters were completed during the summers of 2009 and 2010 in three boreal lakes (Lakes 373, 375, and 626) at the Experimental Lakes Area (ELA), Northwestern Ontario (Fig. 1). All three lakes are small (~20 – 30 ha), have similar morphometric characteristics, are closed to angling, and Lake Trout is the top predator (Blanchfield *et al.* 2005; Wall and Blanchfield 2012).

Tagged fish in all three lakes were detected and positioned using radio-acoustic positioning (VRAP) systems (VEMCO, Nova Scotia, Canada). Details of the VRAP systems have previously been described for Lakes 375 and 373 (Blanchfield *et al.* 2005; 2009). In the spring of 2010, the two VRAP systems from Lake 375 were moved to the two main basins of Lake 626 (Fig. 1). For field estimation of SS, we used only fish detections that occurred within the triangle formed by the VRAP buoys, where positioning accuracy by the VRAP system is highest [1-2 m to ~5 m] (Klimley *et al.* 1998; O'Dor *et al.* 1998; Blanchfield *et al.* 2005).

Swimming speeds of wild fish were estimated from position locations provided by the VRAP system, and the relationship between these estimates and the raw values of acceleration reported by the transmitters was assessed. Similar to Blanchfield *et al.* (2005), the 3-dimensional rate of fish movement between successive position detections was used to estimate swimming speeds (details in *S4*). Values of SS were estimated over the smallest time interval allowed by the reporting rate of the depth sensor (~ 4 min; see Table 1). Therefore, we only used sequential positions (of depth, acceleration, and depth) within 2 min of each other, with no intermediate missing positions, to ensure that the acceleration data reflected the activity pattern of the fish over that interval.

In Lake 375, a single fish was implanted with a short-delay transmitter (25 s random delay) and two VRAP systems positioned this fish (every ~30 s) during the summer of 2009.

Data from this transmitter permitted us to determine fish movements on a shorter time scale and evaluate the degree to which fish speeds might be underestimated by assuming linear movement between locations points provided every ~ 2 min by long-delay transmitters. To do this, we identified time intervals that had three or more sequential position detections, which provided sets of time intervals (ranging from ~ 55 s to ~ 360 s) that contained from 3 to 13 successive locations, with each location separated by ~ 30 s. For each time interval, we calculated the SS of the fish by two methods: (i) a detailed method (labeled short-SS) using the sum of all the 3-dimensional linear distances between each pair of sequential detections within the time interval; and (ii) a coarse method (labeled long-SS), using the 3-dimensional linear distance between the first and last detection in the interval. We then explored: (a) how the SS ratio (short-SS/ long-SS) varied with the length of the interval used for the long-SS estimates and (b) the relationship between the SS ratio and the transmitter-reported acceleration.

A method to convert acceleration data into metabolic rates of wild fish

To demonstrate the applicability of acceleration transmitters in the field with an example from natural populations, Lake Trout telemetry data from Lakes 373 and 626 were analyzed. To simplify this worked-example, we selected a period of 20 days during the summer (July 26 to August 14, 2010) when limnological conditions in both lakes were similar. Acceleration data from 10 fish per lake (Table 1) were translated to metabolic costs, and the overall cost of activity was compared between lakes. In order to obtain metabolic rates we had to consider several different factors (see also S5):

i) The total metabolism (M_{tot}) can be expressed in terms of standard (M_{std}) and active metabolism, and for the latter, swimming metabolism (M_{swim}) is the largest component, so that $M_{\text{tot}} = M_{\text{std}} + M_{\text{swim}}$.

ii) Metabolic processes are related to temperature (T), particularly in ectothermic organisms like fish. Temperature is the main factor influencing M_{std} , however, swimming costs have been found to be relatively independent of temperature (Johnson *et al.* 1998; Claireaux *et al.* 2006; Hein and Keirsted 2012). This is explained through the fact that the energy needed to move a body through water with relatively unchanged density (the change in water density from 4 °C [$1000 \text{ kg}\cdot\text{m}^{-3}$] to 20 °C [$998.23 \text{ kg}\cdot\text{m}^{-3}$] is $\sim 0.02\%$ of the density at 4 °C) is mainly explained by the surface area of the moving body and the speed at which it is moving (Fish 2010). Supporting this assumption, Wilson *et al.* (2013) found that, for a related salmonid (Sockeye Salmon, *Oncorhynchus nerka*), the change in metabolic rate with an increase in swimming speed was independent of temperature over the range from 12 – 18 °C, which is within the optimum for the species.

iii) Metabolic processes are related to body size (W) (Peters 1983), typically following an allometric relationship with $M_{\text{std}} = a \cdot W^b$. We applied the exponent $b = 0.85$, which has been previously used to standardize estimates of M_{std} for differences in body size among studies on Lake Trout (Beamish *et al.* 1989; Evans 2007). To adjust estimated swimming costs for differences in body size among individuals, we used the surface area dependence of power loss due to drag as a guideline. We considered that the surface area of a body that changes in size but maintains its basic shape and density would be roughly proportional to $W^{0.67}$ [$\sim c \cdot W^{2/3}$] (e.g. Peters 1983) and used this form of weight dependence to adjust estimated swimming costs for size differences.

Given all these assumptions, and to translate field (f) acceleration values into metabolic costs using the equations obtained in the laboratory (l), we needed to account for the temperature and size-dependence of Mstd, and the size-dependence of Mswim. For field estimates of Mstd, we began with the equation for Mstd proposed by Evans (2007) and then included the allometric dependence on body weight with exponent of 0.85 to arrive at the following equation for a Lake Trout of weight W_f exposed to temperature T_f (details in S5):

$$Mstd_{(W_f, T_f)} = (46.072 \cdot e^{0.0607 \cdot T_f}) \cdot (0.1) \cdot \left(\frac{W_f}{0.1}\right)^{0.85}$$

Similarly, to calculate Mswim of a fish of weight W_f , swimming with acceleration A_i , we assumed temperature-independent costs, and an allometric exponent of 0.67 for drag effects to arrive at the following equation:

$$Mswim_{(A_i, W_f, T_f)} = Mswim_{(A_i, W_l)} \cdot \left(\frac{W_f}{W_l}\right)^{0.67}$$

where W_l is the weight of laboratory-fish. Therefore, combining these two equations for Mstd and Mswim, it is possible to estimate the total field metabolic costs incurred by tagged fish. Furthermore, to facilitate a more ecologically meaningful comparison of typical costs experienced by Lake Trout living in different lakes, we used a cost index (CI), based on the ‘activity multiplier’ parameter of the widely-used Wisconsin bioenergetics model (Kitchell *et al.* 1977; Hanson *et al.* 1997):

$$CI_{(A_i, W_f, T_f)} = \frac{Mswim_{(A_i, W_f, T_f)}}{Mstd_{(W_f, T_f)}}$$

which measures activity costs in terms of multiples of standard metabolic costs. This index provides a standardized measure of activity that allows for comparison of different populations.

The laboratory calibration work performed in this study covered the full range of acceleration values observed in the field. However, in the laboratory (i) acceleration values ~ 8 a.u. were typically generated by fish observed to be at rest or not actively swimming; (ii) acceleration values substantially less than 8 a.u. were rarely observed; (iii) when our empirical M_{tot} -acceleration regression equations were used to estimate M_{tot} for acceleration reports < 8 a.u., quantities less than the M_{std} value from Evans (2007) equation were obtained. All of these findings suggest that acceleration values < 8 a.u. are typically generated by fish at rest.

Therefore, we filtered our field data accordingly, assigning $M_{\text{tot}} = M_{\text{std}}$ for all observations of acceleration < 8 a.u. For the rest of the range of acceleration values, we were able to translate them into oxygen consumption values without extrapolating any of the observed calibration functions (*i.e.* observed acceleration to estimated uniform [steady-state] SS; estimated steady-state SS to oxygen consumption) beyond the range of data from which they were derived. After the metabolic rates were calculated, the M_{swim} and the CI for acceleration values < 8 a.u. produced zero values (because if $M_{\text{tot}} = M_{\text{std}}$, then $M_{\text{swim}} = 0$ and $\text{CI} = M_{\text{swim}}/M_{\text{std}} = 0$).

Given this, we decided to divide the data into two segments: (i) 'inactive' behaviour (acceleration ≤ 8 a.u.) and (ii) 'active' behaviour (acceleration > 8 a.u.) and focus our interpretation on the observed frequency and magnitude of 'active' behaviour.

Statistical analyses

The variables analyzed were log-transformed ($\log_{10}$) to obtain linear and normalized data. For the laboratory and field data, the relationships between variables were tested using Linear

Mixed Models (LMM), with subject (each fish) considered as random factors to account for the lack of independence in the data (Pinheiro and Bates 2000). The best model was selected by evaluating the Akaike Information Criterion (AIC) between several models produced. In the laboratory, SS was treated as the explanatory variable when studying the TBF-SS relationship, the acceleration-SS relationship (particularly its sensitivity to transmitter placement) and the oxygen consumption –SS relationship. However, we set SS as the response variable in the mixed model analyses designed to generate SS-acceleration relationships that could be used to estimate SS in wild fish from reported acceleration values (Warton *et al* 2006). Several covariate structures were assessed depending on the question being addressed. Because relationships obtained on variables transformed to logarithms create biases, we applied the correction proposed by Sprugel (1983) (final regression result is multiplied by a correction factor, calculated from the standard error estimate of the regression) where appropriate. Metabolic rates were compared between lakes using type II ANOVA (Langsrud 2003) that used a Wald test, so chi-squared (X^2) statistics were reported. All the analyses were performed using the R language for statistical computing (R Core Team 2014 - version 3.1.2).

Results

Laboratory experiments

Tagged Lake Trout recovered quickly after surgery (under 5 min), and visual observations showed no stress (*e.g.* bleeding, lack of movement, loss of balance) related to the surgical procedure or to the presence of stitches. One week after surgery, fish were able to swim regularly at most swimming speeds. At slow speeds (approximately $<30 \text{ cm} \cdot \text{s}^{-1}$ or $<0.5 \text{ BL} \cdot \text{s}^{-1}$), there was insufficient drag for fish to engage in active and steady swimming, so speeds lower

than that threshold were not considered in any of our analyses. At fast speeds (approximately $>57 \text{ cm}\cdot\text{s}^{-1}$ or $>1 \text{ BL}\cdot\text{s}^{-1}$), the drag frequently exceeded swimming capacity and fish exhibited erratic, bursting movements. The burst movements were characterized by short intervals of very high TBF interspersed with intervals of ‘glide’ movements at which the SS of fish matched the water flow, although sometimes fish were unresponsive and ‘resting’ at the back grid of the swim tunnel. Additionally, during burst movements, fish frequently swam at the front of the holding compartment, and the reported acceleration always reached the maximum capacity of the transmitter. These results were also omitted from our analyses.

Effect of transmitter position within the body cavity

Visual observations confirmed that all six fish used in this part of our study responded well to having a transmitter positioned in the mid-ventral portion of the body, tethered to the incision, including the three fish implanted with two transmitters. Additionally, we did not observe abnormal behaviours (lack of movement in the swim tunnel, lack of feeding in the recovery tanks) or limited range of movements in these fish compared to the single-tagged fish.

The relationship linking acceleration to SS was evaluated for each fish and transmitter (Table *SI*). On average, the regression parameters described well the positive and linear relationship (mean and standard error for slopes: $0.02 \pm 0.0004 \text{ m}\cdot\text{s}^{-1}$ and for intercepts: $0.74 \pm 0.04 \text{ a.u.}$ with mean coefficients of determination: 0.9 ± 0.02). We pooled the data for the three fish implanted with double-transmitters and evaluated the acceleration-SS relationship using LMM. The best model ($\Delta\text{AIC} = 335$) included random intercepts and slopes for each fish (standard deviation for intercepts was 0.07 and for slopes was 0.0006 and residuals were 0.09) and position of the transmitter (mid or back) was an important factor determining the

acceleration-SS relationship. The linear model fitted to the data from posterior-implanted transmitters showed higher intercept values (test of equal means $p < 0.0001$, Fig. 2) and higher slopes ($p = 0.014$) compared to mid-implanted transmitters. Therefore, TBF-transmitters implanted towards the back of the body cavity were more sensitive to tail movements, although the correlation between mid-location acceleration and SS was still high. When transmitter position was assessed after euthanizing fish at the completion of the exercise experiments, each transmitter had moved backward to the extent permitted by the tether. In addition, in our later formal exercise experiments, assessment of transmitter movement at the end of each set of exercise experiments showed that, for most fish, the transmitter remained at the back of the body cavity throughout the study. Only two fish showed anterior movement of the transmitter, and in both cases they were mature females with body cavities sufficiently expanded by developing eggs to permit the transmitter to move relatively freely within them.

Comparison of TBF, SS and transmitter-based acceleration

Lake Trout TBF increased linearly with increasing water flow (thus SS) in the swim tunnel ($R^2 = 0.87$, $p < 0.001$, $n = 518$, Fig. 3a). Similarly, we found a positive linear relationship between SS (dependent variable) and transmitter-acceleration (independent variable) when a simple linear model was used (regression parameters for each individual fish in Table S2, overall $R^2 = 0.82$, $p < 0.001$, $n = 5272$) and when LMM were used (Fig. 3b). Individual fish were treated as random effects in the LMM, which should account for differences in individual characteristics such body size and a formal test showed no significant interaction ($F = 2.14$, $p = 0.17$) between body size as factor and acceleration as covariate. Logarithmic values of SS and acceleration were

linearly related (ΔAIC from full to reduced model = 2921), with higher values of acceleration predicting higher swimming speeds (Fig. 3b).

Laboratory fish tagged with long-delay transmitters (V9AP) showed similar relationships between SS and acceleration (Fig. S2) when compared to fish tagged with short-delay transmitters (V9A). LMM, where the transmitter type was treated as factor, and the $[\log_{10}]$ of acceleration was treated as covariate, showed similar slopes for both types (the interaction between transmitter type and the covariate was not significant, $p = 0.44$), but higher intercepts for the short-delay transmitter data (LMM model for V9A was $\{\log_{10} [SS+1] = 0.46 \cdot \log_{10} [\text{acceleration}] + 0.91\}$ and for V9AP was $\{\log_{10} [SS+1] = 0.445 \cdot \log_{10} [\text{acceleration}] + 0.91\}$). However, because the effect of the transmitter type was weakly significant ($p = 0.04$) and made only a small improvement in the LMM ($\Delta AIC = 2.3$), transmitter type was not considered as a factor in the final model $\{\log_{10} [SS+1] = 0.45 \cdot \log_{10} [\text{acceleration}] + 0.91\}$.

Oxygen consumption experiments

All fish exercised at $30 \text{ cm} \cdot \text{s}^{-1}$ ($0.5 \text{ BL} \cdot \text{s}^{-1}$) and $57 \text{ cm} \cdot \text{s}^{-1}$ ($1 \text{ BL} \cdot \text{s}^{-1}$) were able to maintain a constant SS for at least one hour, so a steady reduction in DO_2 concentration was observed. Similar to earlier trials, some fish were not able to swim uniformly at fast speeds (around $83 \text{ cm} \cdot \text{s}^{-1}$ or $1.5 \text{ BL} \cdot \text{s}^{-1}$) for a period of time long enough to detect a decrease in the concentration of DO_2 in the water, thus these data were unusable. In general, all fish increased their oxygen consumption (MO_2) when they had to swim faster (Fig. 3c). A LMM fitted to the data (model: $\{\log_{10} [\text{MO}_2] = 1.17 \cdot \log_{10} [\text{acceleration}] + 0.22\}$) suggested that each individual fish had a random intercept with standard deviation of 0.03 and standard deviation of the residuals of 0.06.

Field trials

All wild Lake Trout implanted with activity transmitters were detected by the automated positioning systems. Four fish were excluded from the analyses because of insufficient detections (< 10) within the buoy triad (Table S2). We observed a general increasing trend in calculated swimming speeds as telemetry values of acceleration increased. However, the relationship between SS and acceleration was much more variable for field trials than for laboratory trials (Fig. 4a, b) and SS estimates in the field were lower than the SS observed in laboratory trials. LMM fit to the data from Lake 373 improved when individual fish were considered as random factors ($\Delta AIC = 95.9$; model: $\{\log_{10} [SS+1] = 0.42 + 0.32 \cdot \log_{10} [\text{acceleration}]\}$). However, for L626 the use of a mixed model did not improve the fit ($\Delta AIC = 2$), nevertheless we used this approach because it is appropriate for longitudinal data (model: $\{\log_{10} [SS+1] = -0.01 + 0.64 \cdot \log_{10} [\text{acceleration}]\}$). Pooled data showed a significant effect of lakes in the LMM ($\Delta AIC = 8$ from a model with no distinction between lakes to a model with lake considered as factor). The final model included random intercepts and slopes for each individual fish and the interaction of lakes with the covariate.

We observed a positive linear relationship (equation: $\log_{10} [SS+1] = 0.38 \cdot \log_{10} [\text{acceleration}] + 0.35$; $R^2 = 0.23$, $p < 0.001$, $n = 4330$) between SS, calculated from positional data, and acceleration from a Lake Trout implanted with a short-delay transmitter in Lake 375, that was similar to the relationship obtained from laboratory data. The coefficient of determination reflects the high variation around the regression line, but similar to lakes 373 and 626, a linear model was successful in explaining the relationship between SS and acceleration. The main objective of this single-transmitter trial was to evaluate the assumption of linear movement between position detections. To do this, we compared the SS ratio (short-SS/long-SS,

refer to Methods) applied to increasingly longer time intervals up to (and exceeding) the time interval obtained with the long-delay transmitters (~ 4 min) used in Lakes 373 and 626. As the time interval between successive positional locations increased, the SS ratio increased, reaching a value of ~2 when the time interval approached the 4 min typical of the long-delay transmitters (Fig. 5a); however, this effect tended to disappear at higher acceleration values ($\text{Log}_{10}[\text{acceleration}] > 1.5$, Fig. 5b). To further verify that swimming speeds were underestimated in Lakes 373 and 626 where long-delay transmitters were used, we compared the speeds estimated for fish from those lakes to speeds estimated for the single fish implanted with the short-delay transmitter in Lake 375 (Fig. 6a, b). At acceleration values < 1.5 , SS estimates from all lakes and transmitters increased progressively with increases in acceleration. The speed estimates generated by the long-delay transmitters were ~ 50% of the speed estimates generated by the short-delay transmitters – a result consistent with the relationship in Fig 5a. However, at acceleration values > 1.5 , the relationships among all these quantities changed substantially: (i) the ratio of swimming speeds (short-SS/ long-SS) approached 1 (Fig 5b), and (ii) SS itself was essentially constant at around $10 \text{ cm} \cdot \text{s}^{-1}$ and independent of acceleration (Fig 6a, b).

Metabolic demands of two natural populations of wild fish

The acceleration data reported by the transmitters implanted in wild Lake Trout covered the range of possible values for these transmitters (2 – 255 a.u.), which represented swimming modes from slow to fast. Rapid increases in acceleration to the maximum reported by the transmitters (*i.e.* possible bouts of burst swimming) were reported in both lakes. Using the methodology we proposed, reported values of acceleration were converted to metabolic costs (Mstd, Mswim and Mtot) and we found significant between-lake differences in the metabolic

costs incurred by Lake Trout. Specifically, Lake Trout in Lake 373 exhibited active behaviour (acceleration > 8 a.u.) more frequently (79%) than fish in Lake 626 (64%) (Fig. 7a). Furthermore, we calculated the cost index (CI) for when Lake Trout showed active behaviour in Lakes 373 and 626 (Fig 7b). We found a significantly greater CI for fish in Lake 373 ($X^2 = 7.06$, $df = 1$, $p = 0.008$ for the one-way type-II ANOVA evaluating differences between CI with lake as factor) than that exhibited by Lake 626 fish (Fig. 7b). Overall, Lake Trout in Lake 373 exhibited more frequent and more intense activity than fish in Lake 626, and consequently incurred a greater metabolic cost of day-to-day activities.

Discussion

Effect of transmitter position within the body cavity

The ability of activity transmitters to sample the acceleration of aquatic animals is based on their capacity for measuring body movement while swimming. Depending on their morphology and type of swimming behaviour, each fish species accentuates the use of a different set of body parts for locomotion (*i.e.* whole body, pectoral fins, caudal fin) and has specific kinematics (Wardle *et al.* 1995). Thus, to use TBF-transmitters to describe the energy expenditure of aquatic organisms, we must evaluate how to properly insert the transmitter to optimize the sampling of acceleration, which then provides a better estimate of SS. We evaluated the effect of transmitter position in the body cavity and found that posterior-positioned transmitters were more responsive to the amplitude of the swimming movements than mid-positioned transmitters (Fig. 2). This finding is consistent with the swimming kinematics of Lake Trout observed in the laboratory: the caudal fin is the main propulsor; it makes the greatest contribution to thrust (Webb 1984) compared to anterior parts of the body. In the field, Lake

Trout are expected to swim similarly, although they could increase the use of their paired fins for breaking and turning, particularly at slow speeds. For these cases, the placement of posterior-positioned transmitters would increase the chances of detecting a small movement. Additionally, this species is an active top predator – it is rarely subject to predatory attacks and it typically swims steadily, using its tail to provide most of its locomotive force. Consequently, transmitters that measure TBF should be implanted as far back within the body cavity as possible with the accelerometer end directed towards the tail of the fish, where the swimming movements of the tail can be maximally detected.

We also evaluated the tethering requirements for keeping these types of transmitters in place. We determined that tethering was not required as transmitters were kept at the back of the fish from natural swimming movements. Examination of fish (males and females) that had been tagged and exercised for two weeks provided little evidence of transmitter movement: (i) the organs surrounding the transmitters were marked in ways that indicated prolonged pressure from the transmitter; and (ii) frequently, fat tissue had engulfed the transmitter, holding it in place in the body cavity. However, reproductive females may pose a greater challenge, because the transmitter may be forced forward when the body cavity is expanded with egg production and subsequently move backwards after spawning. In such cases the need for consistent data might require use of a tether to constrain transmitter movement in the body cavity. Despite this, our results showed that for those trials where the transmitter was implanted forward in the body cavity, the acceleration reported by the transmitter was still positively associated with the SS of the fish (Fig. 2). Therefore these data could still be used to track relative changes in both SS and metabolic demand, as long as all fish have the transmitters in the same position within the body cavity.

As a result of our study, we recommend standardizing the technique for implanting TBF activity transmitters to provide a consistent sampling of acceleration. For juveniles and for males, we recommend simplifying the surgical procedure by implanting untethered transmitters as far back within the body cavity as permitted by the fish, with the accelerometer end directed towards the tail of the fish. For females with developing eggs, tethering of the transmitter in the body cavity should be considered and, if used, tethering of the rest of the sample fish should be performed to standardize both the surgical technique and the expected relations linking acceleration to SS and metabolic rate.

Relationships between TBF, SS, Transmitter-Based Acceleration, and Oxygen Consumption

In the laboratory, we tested the relationship between TBF, SS, and acceleration for Lake Trout, and we found that all those variables increased in parallel (Fig. 3a, b). We also examined the relationship between oxygen consumption and SS and found a positive association (Fig. 3c). These results agree with what has been reported by Wilson *et al.* (2013) for Sockeye Salmon, where the authors also obtained positive associations between all these variables. Similarly, Payne *et al.* (2011) studied the association between SS, oxygen consumption and acceleration in cuttlefish using TBF-transmitters, and they also found positive associations between these variables in this kinematically different species. Our data add to a growing body of evidence that TBF transmitters provide an accurate method by which to measure fish movement, and thus provide a means to measure the metabolic costs of activity in wild fish. Performance will be influenced by the size of the transmitter (Perry *et al.* 2013), so ideally small transmitters (less than 1% tag-to-body mass ratio) should be used to avoid imposing additional burden on tagged fish.

For fish tagged in the field, we also obtained a positive linear relationship between SS and acceleration. The slopes of field-based and laboratory-based estimations were similar (Fig. 4a, b), supporting the direct relationship between both variables. However, the variability around the regression line was higher for field-based compared to laboratory-based results and had lower intercepts. These results are consistent with the following:

1) In the field, long-delay transmitters that reported interspersed values of depth and acceleration, with mean reporting interval of 120 s, were used. Acceleration was not continually sampled between detections; instead the transmitter averaged acceleration over the first 45 s of each ~4 min reporting period. In this setting, we estimated SS indirectly using location data that was reported at relatively long time intervals. In the laboratory, the SS-acceleration relationship was estimated by direct observations of SS, where fish were swimming constantly and uniformly (steady-state swimming behaviour). In the field, we assumed similar behaviour, which is reasonable if the time interval between detections is not long and if the fish swims with a regular motion (Rowcliffe *et al.* 2012). However, this assumption is likely violated in the wild when activities such as foraging and escape behavior result in short periods of highly variable activity. Therefore, in the field, if fish movement during the acceleration-sampling period is not representative of the entire period between fish detections, estimates of SS will diverge from those based on laboratory conditions, thus contributing to the variability in field-observations.

2) In the field, SS was estimated by assuming linear movement between position detections, which is the minimum possible distance swum by the fish over a given time interval. The movement of organisms must be modeled on a very short spatial-temporal scale for the straight-line assumption to be biologically correct (Turchin 1998). However,

the increased frequency of data collection may result in simultaneous reporting ('collisions') by multiple transmitters, leading to information loss; autocorrelation and location error may also obscure the biological significance of the results (Fieberg and Ditmer 2012). Therefore, substantial error may stem from violation of the assumption that fish move in a linear path over relatively long time periods (~4 min) – real organisms rarely behave in such a simple fashion (Turchin 1998; Rowcliffe *et al.* 2012). This issue is further explained below.

3) Positioning accuracy of the telemetry system represents a source of error. Although we selected detections located within the highest accuracy area of the VRAP, positioning errors can lead to discrepancies between real speed and estimated speed within a time interval (Jerde and Visscher 2005).

Using the short-delay transmitter in the wild, we demonstrated that the linear movement assumption indeed underestimated the distance traveled by Lake Trout implanted with long-delay transmitters by ~2 times (Fig. 5a). We also found that this effect tended to disappear at high acceleration levels (Fig. 5b). This assumption was further examined by direct comparisons of SS-acceleration relationships for wild fish implanted with long and short delay transmitters (Fig. 6a, b). We did obtain underestimation of swimming speeds; however, it was not consistent across all values of acceleration: underestimation was obvious for [Log₁₀] acceleration values lower than 1.5. All of these results are consistent with the following interpretation: (i) lower acceleration values are generated by fish swimming in a steady-state mode, maintaining a relatively constant TBF and a relatively high turning frequency over the 120 s location reporting interval used by the long-delay transmitters; (ii) at higher acceleration values, fish adopt a 'burst-and-glide' swimming pattern that is characterized by bursts of high TBF, interspersed with

intervals of very low TBF (this behaviour was observed and recorded on film in the laboratory when fish were exercised at high speeds); (iii) the ‘burst-and-glide’ swimming pattern is accompanied by a relatively low turning frequency over the 120 s location reporting interval used by the long-delay transmitters. Given the characteristics of a ‘burst-and-glide’ swimming pattern, we would expect to see wide variation in reported acceleration values when this behaviour is adopted because the acceleration sampling interval (45 s) is much shorter than the acceleration reporting interval (~240 s) and therefore the degree to which the sampling interval captures intervals of burst and/or glide levels of acceleration will vary randomly from one acceleration reporting interval to the next. Also, since the high activity levels associated with burst behaviour can only be sustained for short time periods (Beamish 1978; Kolok 1999; and our laboratory observations), the speed estimated from position locations recorded at fixed intervals would tend to reach a plateau (*e.g.* Fig 6*a, b*). Wilson *et al.* (2013) found such bursting behaviour at high acceleration values, and previous studies in Lake Trout (Thorstad *et al.* 2000; Dunlop *et al.* 2010) have described bursting behaviour for this species in laboratory and wild settings.

Fish swimming behaviour in the wild is complex. They can combine resting, active, and burst-glide behaviours over varied time periods (Dunlop *et al.* 2010). Therefore, studies that use telemetry-based positional data to estimate swimming speeds in fish can benefit from the use of acceleration-transmitters to provide additional information on the kinds of swimming behaviour being used. An additional benefit of using acceleration-transmitters in the field is that the data they provide can be used to estimate metabolic rates through the relationships that link acceleration and SS to MO_2 (Wilson *et al.* 2006; Payne *et al.* 2011; Wilson *et al.* 2013). In our laboratory study, we observed an increase in MO_2 as SS increased (Fig. 3*c*), with values within

the range expected for Lake Trout as provided by Evans (2007). There was variability in MO_2 at speeds higher than $1 \text{ BL} \cdot \text{s}^{-1}$, which could be explained by irregular swimming behaviours at fast speeds. At higher speeds, fish were frequently tired and did not swim at the speed set for the swim tunnel, or they frequently engaged in burst-glide swimming behaviour. As well, sometimes fish were exhausted before reaching the faster speeds, so we could not complete that particular exercise trial. While we did not use data from those types of swimming behaviours where fish were not steadily swimming, the fish that did complete the swimming trials could have been operating near their exhaustion point (Hammer 1995). Regardless of the variation in MO_2 , we did observe a strong positive relationship between this variable and the SS of fish, which supports previous observations (Payne *et al.* 2011; Wilson *et al.* 2013) where speed can be used as a predictor for metabolic rates.

Previous studies have shown that SS ($\text{cm} \cdot \text{s}^{-1}$), body length (thus weight) and MO_2 are interrelated as follow: i) smaller fish swim slower than larger fish, but they swim more actively, so larger fish attain faster absolute speeds but small fish swim at faster relative speeds (Bainbridge 1958); ii) smaller fish consume more oxygen per unit weight compared to large size fish (Beamish 1964). The range of body sizes used in our experiments was sufficiently narrow that body size effects were indistinguishable from the random variation inherent in our experimental design. This was tested formally and no effect of size was observed in any of our results. In studies involving the comparison of fish over a wider size range, the companion calibration study should include fish that span the size range of interest so that the influence of size can be evaluated directly.

Metabolic demands of two natural populations of wild fish

The novel method we proposed to convert acceleration data from implanted transmitters into metabolic rates of free-ranging fish allowed us to study the metabolic demands of two populations of wild fish. This offers a new approach for studying bioenergetics of free-ranging fish through acceleration telemetry that promises to be an improvement to the classical used bioenergetics models. Based on the results presented in this study, Lake Trout locomotor state was estimated to be inactive or active. Dunlop *et al.* (2010) also observed this kind of behaviour for Lake Trout. They described fish moving with slow speeds vertically and horizontally, then initiating a period of fast swimming and then returning to a relatively inactive state. In our study, during periods of inactivity, which were characterized by low acceleration values ($A \leq 8$ a.u.), we estimated that most of the oxygen consumed would be invested in the basic biological functions (Mstd) and small or absent locomotor movements would be present. In contrast, periods of activity were characterized by dynamic movements, in which fish spent energy on both Mstd and significant levels of Mswim. Demonstrating the applicability of this novel method, we found that Lake Trout were active more frequently in Lake 373 than in Lake 626. Consistent with this, in Lake 373 the median CI during active periods was higher than in Lake 626 (Fig. 7b). This indicates that, on average, fish in Lake 373 spend more energy when actively swimming than fish in Lake 626. The skewness of the distribution in Fig. 7b also shows that there are fish in both lakes that spend energy swimming at around one to two multiples of their standard metabolism. They can even reach CI values > 8 , however these high energy-requiring activities have a low frequency of occurrences. We evaluate the possible causes for the inter-population difference in the activity rate of fish living in these lakes in a future manuscript.

In this study, we have demonstrated how acoustic transmitters designed to detect and report the acceleration associated with tail movements can be used to estimate the TBF, SS and

664 oxygen consumption of tagged Lake Trout under both laboratory and field conditions. In
665 addition, we have developed a framework, consistent with traditional bioenergetics models, that
666 permits conversion of reported acceleration values into estimates of the metabolic costs
667 experienced by free-ranging fish. We have shown that application of these methods can reveal
668 consistent, population-level differences in the metabolic costs experienced by Lake Trout living
669 in natural environments. These differences can be driven by population differences in both
670 abiotic (*e.g.* temperature, Tunney *et al.* 2014) and biotic (*e.g.* available prey, Giacomini *et al.*
671 2013) factors and can significantly influence Lake Trout life histories (Krohn and Boisclair
672 1994; Rennie *et al.* 2005; Shuter *et al.* 2005), habitat selection and the attainable fitness of a
673 given population (Plumb *et al.* 2014). We will explore some of these effects in detail in future
674 studies.

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List of Tables

Table 1 Source of Lake Trout, sample size (*n*), mean fork length (FL) and weight (W) (range in parenthesis) into which acoustic transmitters with acceleration (A) and pressure (P) sensors were implanted. The delay length (minimum – maximum) between successive transmissions and the acceleration sampling time (AST) are presented for each transmitter; in addition, the mean acceleration reporting time (ART) and the mean location reporting time (LRT) are included. All transmitters sampled acceleration at 10 Hz.

Lake	<i>n</i>	FL (mm)	W (g)	Transmitter sensors	Delay (s)	AST (s)	ART (s)	LRT (s)
Laboratory-trials – transmitter placement								
Opeongo / Louisa	6	512 (479-554)	1657 (1319-2137)	A	25 – 25	20	30	-
Laboratory-trials – transmitter calibrations								
Opeongo / Louisa	9	480 (448-537)	1227 (879-1619)	AP	100 – 140	45	240	-
Opeongo / Louisa	15	480 (437-534)	1341 (938-1823)	A	25 – 25	20	30	-
Laboratory-trials – oxygen consumption								
Opeongo / Louisa	16	507 (437-549)	1551 (1002-1997)	-	-	-	-	-
Field-trials – Experimental Lakes Area								
375	1	399	655	AP	20 – 30	17	60	30
373	10	403 (354-454)	652 (499-785)	AP	100 – 140	45	240	120
626	10	419 (356-540)	838 (487-1848)	AP	100 – 140	45	240	120

Figure captions

Fig. 1. Lake Trout implanted with acceleration transmitters were monitored by radio-acoustic positioning telemetry in each of three lakes at the Experimental Lakes Area, Canada (inset, star). The area of highest positioning accuracy by each telemetry system is represented by the triangle connecting hydrophone buoys (filled circles) in each lake.

Fig. 2. Linear relationship between acceleration and swimming speed for laboratory Lake Trout implanted with transmitters in different positions within the body cavity. Three fish were tagged with double transmitters: mid-ventral (midA – closed circle and dashed black line) and posterior (backA – open circle and dotted black line). Three separate fish were tagged with single transmitters implanted in the mid-ventral position (midB – open triangle and solid gray line). The lines represent the linear relationships obtained with linear mixed models, with fish considered as random factors.

Fig. 3. Linear relationships between the variables measured in the laboratory at ambient water temperature (11.76 ± 1.26 °C): (a) tail-beat frequency (TBF) and swimming speed (SS); (b) SS and acceleration; and (c) oxygen consumption (MO_2) and SS. Solid lines in all the panels represent the linear mixed models (LMM) fitted to data with individual fish considered as random factor. Dotted lines in (a) and (c) represent the 95% confidence intervals for the regression lines. The equations obtained with LMM to describe the linear relationships are presented below each panel.

Fig. 4. Linear representation of the relationship between Lake Trout swimming speed (SS) estimated from position telemetry in the field and acceleration reported by transmitters. Panel (a) represents Lake 373, and (b) Lake 626. All data used in each model are plotted, along with the linear relationship obtained by linear mixed models. Axes scales cover the range of field data and

the relationship obtained in the laboratory is represented with a dashed line and shading to facilitate visual comparison. The equations obtained for each model are presented as well.

Fig. 5. (a) The SS ratio (short-SS/long-SS) is plotted against the time interval used to calculate the long-SS. This ratio (where short-SS is the sum of linear distances between each detection over time interval t and long-SS is the linear distance between the positions at the beginning and end of time interval t) is a measure of the bias in the estimate of SS arising from the assumption that fish swim in straight line between successive positions. The median value of this bias increases progressively ($R^2 = 0.87$, $p = 0.004$, $n=6$) with the length of the time interval showing that, as the length of the interval increases, the straight-line distance between positions at the start/end of the interval progressively under-estimates the ‘true’ distance fish travel over the interval. The range of observed bias values also tends to increase with the duration of the interval. **(b)** The bias in SS estimates is plotted against acceleration for a fixed time interval of 3.76 min (*i.e.* all data from box 3.76 in panel a). With the time interval fixed, the median bias decreases progressively toward 1.0 ($R^2 = 0.91$, $p < 0.001$, $n = 7$), suggesting that higher observed acceleration values over a fixed interval are associated with straighter travel over that interval.

Fig. 6. Box plots representing the relationship between swimming speed (SS) and acceleration for long- and short-delay V9AP transmitters in the wild. The light-grey lines above the boxplots represent laboratory data. Dark grey boxes represent the short-delay transmitter used in Lake 375 (speeds calculated over an average of 1 min), and light grey boxes represent the long-delay transmitters used in (a) Lake 373 and (b) Lake 626. SS were calculated over an average time interval of 4 min for the long-delay transmitters. For $[\text{Log}_{10}]$ acceleration values < 1.5 a.u., SS estimates from the long-delay transmitters in Lakes 373 and 626 were always lower than those

estimated from the short-delay transmitter in Lake 375. All field-based estimates of SS were less than laboratory-based estimates.

Fig. 7. (a) The proportion of detections that indicated active behaviour by Lake Trout in Lakes 373 and 626. (b) Distribution of cost index values ($CI = M_{swim}/M_{std}$, where M_{swim} is the swimming metabolic rate and M_{std} is the standard metabolic rate) observed during active behavior for all fish in each lake (10 fish per lake, mean observations per fish = 3430). Fish in Lake 373 were active more frequently and showed higher median CI.

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Fig. 1.

1001

1002 **Fig. 2.**

1003

a. TBF - SS

SS (cm·s⁻¹)

TBF =

$$47.09 + 1.11 \cdot SS$$

b. SS – acceleration

Log₁₀ [acceleration (a.u.)]

Log₁₀ [SS] =

$$0.91 + 0.46 \cdot \text{Log}_{10} [\text{acceleration}]$$

c. MO₂ – SS

Log₁₀ [SS (cm·s⁻¹)]

Log₁₀ [MO₂] =

$$0.22 + 1.17 \cdot \text{Log}_{10} [SS+1]$$

1004

1005 **Fig. 3.**

Fig. 4.

Fig. 5.

1011

1012 **Fig. 6.**

1013

1014 **Fig. 7.**