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

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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 ± 0.03 body lengths s^{-1} and cost of transport was 3.39 ± 0.17 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.

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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