

Accelerometer-derived activity correlates with volitional swimming speed in lake sturgeon (*Acipenser fulvescens*)

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Abstract: Quantifying fine-scale locomotor behaviours associated with different activities is challenging for free-swimming fish. Biologging and biotelemetry tools can help address this problem. An open channel flume was used to generate volitional swimming speed (U_s) estimates of cultured lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) and these were paired with simultaneously recorded accelerometer-derived metrics of activity obtained from three types of data-storage tags. This study examined whether a predictive relationship could be established between four different activity metrics (tail-beat frequency (TBF), tail-beat acceleration amplitude (TBAA), overall dynamic body acceleration (ODBA), and vectorial dynamic body acceleration (VeDBA)) and the swimming speed of *A. fulvescens*. Volitional U_s of sturgeon ranged from 0.48 to 2.70 m·s⁻¹ (0.51–3.18 body lengths (BL)·s⁻¹). Swimming speed increased linearly with all accelerometer-derived metrics, and when all tag types were combined, U_s increased 0.46 BL·s⁻¹ for every 1 Hz increase in TBF, and 0.94, 0.61, and 0.94 BL·s⁻¹ for every 1g increase in TBAA, ODBA, and VeDBA, respectively. Predictive relationships varied among tag types and tag-specific parameter estimates of U_s are presented for all metrics. This use of acceleration data-storage tags demonstrated their applicability for the field quantification of sturgeon swimming speed.

Key words: accelerometer, biologging, lake sturgeon, *Acipenser fulvescens*, swimming speed, tail-beat frequency.

Résumé : La quantification du comportement locomoteur fin associé à différentes activités des poissons nageurs constitue un défi de taille. Des outils de mesure embarquée (« biologging ») et de biotéléométrie peuvent aider à résoudre ce problème. Un canal en eau libre a été utilisé pour produire des estimations de la vitesse de nage (U_s) volontaire d'esturgeons jaunes (*Acipenser fulvescens* Rafinesque, 1817) d'élevage, et ces vitesses ont été jumelées à des paramètres simultanés de l'activité tirés de mesures d'accéléromètre obtenues de trois types d'étiquettes enregistreuses de données. L'étude a tenté de déterminer si une relation prédictive peut être établie entre quatre paramètres d'activité différents (fréquence des battements de la queue (TBF), amplitude d'accélération des battements de la queue (TBAA), accélération dynamique globale du corps (ODBA) et accélération dynamique vectorielle du corps (VeDBA)) et la vitesse de nage d'*A. fulvescens*. La fourchette d' U_s volontaires des esturgeons était de 0,48 à 2,70 m·s⁻¹ (0,51–3,18 longueurs du corps (LC)·s⁻¹). La vitesse de nage augmentait linéairement avec l'augmentation de tous les paramètres tirés des mesures d'accéléromètre, et quand tous les types d'étiquettes étaient combinés, U_s augmentait de 0,46 LC·s⁻¹ pour chaque augmentation de 1 Hz de la TBF, et de 0,94, 0,61 et 0,94 LC·s⁻¹ pour chaque augmentation de 1g de la TBAA, de l'ODBA et de la VeDBA, respectivement. Les relations prédictives variaient selon le type d'étiquettes, et des estimations des paramètres d' U_s pour différentes étiquettes sont présentées pour tous les paramètres d'activité. Cet usage d'étiquettes enregistreuses de données d'accélération démontre qu'elles peuvent être appliquées à la quantification sur le terrain de la vitesse de nage des esturgeons. [Traduit par la Rédaction]

Mots-clés : accéléromètre, mesure embarquée, esturgeon jaune, *Acipenser fulvescens*, vitesse de nage, fréquence des battements de la queue.

Introduction

Allocation of an organism's time and energy to different behaviours can influence survival and fitness, and ultimately influence population dynamics (Morales et al. 2010; Tomlinson et al. 2014). As such, the rate at which animals expend energy is a key component to understanding how they interact with their surrounding environment. Activity, primarily derived through locomotion,

represents the principal energy cost in addition to basic metabolism, with field metabolic rates typically three times that of basic metabolism (Alexander 1999). Biotelemetry and biologging tools show promise for the field measurement of key variables including activity and specific energy metabolism in aquatic animals (Cooke et al. 2004a; Castro-Santos and Haro 2006), but can often be inaccurate, imprecise, or unreliable (Geist et al. 2002; Cooke et al. 2004b; Enders et al. 2008). Accelerometers, which provide a mea-

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sure of individual locomotory activity, are increasingly being used in aquatic environments (e.g., using telemetry: Lowe et al. 1998; O'Toole et al. 2010; Murchie et al. 2011; using biologgers: Watanabe et al. 2012; Brownscombe et al. 2013). Laboratory calibrations indicate strong correlations between accelerometer-derived metrics of activity and both swimming speed (U_s) and oxygen consumption (Mo_2) for a range of aquatic taxa (e.g., elasmobranchs: Gleiss et al. 2010; cephalopods: Payne et al. 2011; fish: Clark et al. 2010; Wilson et al. 2013). When paired with field deployments, these calibrations have also enabled quantification of energy use in the wild for the same range of taxa (Payne et al. 2011; Semmens et al. 2013; Wilson et al. 2013).

Interest in the comparative swimming ability of aquatic taxa, in terms of energetics, speed, and endurance, has resulted in the widespread use of swim tunnels where individuals are forced to swim against known water velocities to maintain position (Beamish 1978; Hammer 1995). Swim tunnels are also used in the calibration of accelerometer data with U_s and (or) Mo_2 . However, practical limitations exist based on the size of study animals and corresponding test facilities. For example, Lowe (1996) demonstrated reduced tail-beat amplitude (TBA), and corresponding stride length, associated with the restricted swimming of scalloped hammerhead sharks (*Sphyrna lewini* (Griffith and Smith, 1834)) in a swim tunnel compared with free-swimming. In a later study on the same species, Gleiss et al. (2010) demonstrated that the logged acceleration values from exercised sharks in a swim tunnel did not adequately represent the range of speeds (and corresponding acceleration values) observed in free-swimming individuals. Swim tunnel experiments are typically restricted to smaller species and juveniles of large species, and it is sometimes necessary to conduct in situ calibrations in the field for larger animals and (or) borrow established relationships from other species (e.g., Semmens et al. 2013). There is also increasing evidence that the relationships developed from forced swimming experiments may not be directly transferable to free-swimming animals. For example, Peake (2004) identified that swimming performance measures from a swim tunnel were a poor predictor of passage ascent when small-mouth bass (*Micropterus dolomieu* Lacepède, 1802) were faced with a velocity challenge and advised caution in transferring laboratory data to field applications. The use of open channel flumes of an appropriate size so as not to restrict TBA and that rely on volitional U_s and behaviours hold promise for the determination of more field relevant U_s and corresponding acceleration-derived metrics (e.g., Castro-Santos 2005; Castro-Santos et al. 2013).

Sturgeon are long-lived organisms of the Acipenseridae family that occur in large rivers spanning the temperate zones of Asia, Europe, and North America and often represent the largest animals in a freshwater fauna (Bemis and Kynard 1997). They represent an evolutionally basal group of fishes—fused fin rays mean that they have limited ability to manipulate their fins and locomotion is primarily driven by body undulations and associated movements of median and paired fins (Breder 1926; Wilga and Lauder 1999; Liao and Lauder 2000). Sturgeon exhibit a number of morphological limitations including a comparatively high drag resulting from body form and external scutes, as well as low thrust resulting from their heterocercal tail (Webb 1986). Combined with a relatively limited capacity for high-speed swimming resulting from a poor aerobic capacity (Peake et al. 1997), these factors collectively contribute to the reduced swimming capacity of sturgeon with, for example, similarly sized salmonids. These and other observations have led to the widespread perception of sturgeon as relatively poor swimmers. However, sturgeon often spawn in the moderate to high-velocity regions of large rivers (e.g., Thiem et al. 2013) preceded in many cases by large-scale migrations (Auer 1996) that may sometimes include passage through natural rapids (e.g., Welsh and McLeod 2010). Laboratory studies indicate that sturgeon are capable of short periods of energetically demanding burst swimming when traversing high-

velocity regions, followed by utilisation of low-velocity regions for recovery (Webber et al. 2007; Cocherell et al. 2011). In some instances, benthic station holding is used in high-velocity regions as an energy conservation strategy (e.g., Adams et al. 2003; Geist et al. 2005). Alternatively, individuals may actively seek a path of least resistance (e.g., McElroy et al. 2012). In either case, some measure of the rate of work is required via the monitoring of individual activity to estimate and better understand energy expenditure and its role in limiting movement and distribution.

Before using accelerometers to determine the rate at which animals expend energy, it is necessary to validate relationships on a species-specific basis (Halsey et al. 2011) and an accelerometer-placement-specific basis (Gleiss et al. 2011). Doing so enables researchers to apply such devices to free-ranging animals to quantify behaviour and estimate energy expenditure in the field. The objectives of this study were to measure a range of sturgeon U_s and to determine whether accelerometer-derived metrics (tail-beat frequency (TBF), tail-beat acceleration amplitude (TBAA), overall dynamic body acceleration (ODBA), and vectorial dynamic body acceleration (VeDBA)) accurately represent U_s and thus serve as a proxy for the measurement of activity-specific behaviours. A secondary objective was to determine whether the relationships between U_s and accelerometer-derived metrics varied among several commonly used tag types. Volitional swimming was used, as it more likely represents the range of U_s attained by free-swimming animals. This study used a widely distributed North American sturgeon species, lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817). This species is of particular interest given its local abundance, existing literature regarding swimming performance and associated Mo_2 , and the postulation that the poor swimming capacity of sturgeon in general elicits a variety of behavioural responses to high velocities including short bursts of high U_s and (or) benthic station holding.

Materials and methods

Trial protocol

An open channel outdoor flume was used to develop relationships between volitional U_s and accelerometer-derived activity metrics in *A. fulvescens*. The flume was located at the US Geological Survey S.O. Conte Anadromous Fish Research Laboratory fish passage complex, Turners Falls, Massachusetts, USA, and was 1 m wide \times 1 m deep \times 20 m long with zero slope. The apparatus was the same as that described by Castro-Santos et al. (2013) and is substantially wider than previously used swim tunnels for similarly sized sturgeon (e.g., 0.3 m diameter swim tunnel: McKinley and Power 1992; 0.56 m diameter swim tunnel: Peake et al. 1997). Ambient river water was supplied to the flume from an adjacent hydroelectric power canal fed by the Connecticut River. Water entered the flume through a 76.2 cm diameter pipe, regulated with a 61.0 cm butterfly valve, into a head tank control structure. Water from the head tank entered the test flume and flow was regulated with a submerged vertical lift gate. Water exited the flume into a large, low-velocity downstream staging area (3.6 m long \times 4.9 m wide \times 1.45 m deep) mounted off-centre from the flume channel and with a floor 12 cm below the floor of the flume. Water was discharged from this staging area via three outlets; water depth in the staging area was regulated using stoplogs (wooden boards positioned in slots at each outlet). Depth and velocity of flow within the flume were regulated using a combination of valve opening, head tank depth, head gate height, and staging area depth. Screens were placed just upstream of the stoplogs. This arrangement kept fish from being swept downstream and helped to prevent them from becoming impinged on screens by distributing discharge over the full depth of the staging area.

Two trials each consisting of slow (~ 0.48 m·s⁻¹), medium (~ 1.00 m·s⁻¹), and fast (~ 1.36 m·s⁻¹) water-velocity treatments were conducted ($n = 6$ trials total) to encourage volitional swim-

Table 1. Details of individual lake sturgeon (*Acipenser fulvescens*) used to quantify the relationship between accelerometer-derived metrics of activity and swimming speed in an open channel flume, using three different types of tags (tag type).

Fish ID	TL (cm)	Mass (kg)	Tag type	Trial					
				1a	1b	1c	2a	2b	2c
1	84	3.4	1				×	×	×
2	81	3.2	1				×	×	×
3	95	4.4	1				×		×
4	87	3.3	1					×	×
5	97	4.9	1					×	
6	97	4.6	2						×
7	91	4.2	2						×
8	87	3.4	2				×		×
9	93	4.9	2				×		×
10	83	3.3	2						×
11	92	3.6	2				×		
12	93	4.8	3		×				
13	98	5.0	3		×				
14	98	5.1	3	×	×	×			
15	90	4.2	3		×				
16	96	4.1	3			×			
U_f (m·s ⁻¹)				0.48±0.00	1.00±0.01	1.36±0.00	0.48±0.01	0.99±0.00	1.38±0.01
z (m)				0.23	0.40	0.41	0.27	0.40	0.40

Note: Hydraulic characteristics for each trial are presented including water velocity (U_f ; mean \pm SE) and water depth (z), with data collected from the centre of the flume and cross-sectional velocity data pooled among depths and flume width locations. Individual ascents for each trial (×) are indicated. Use of TL refers to total length. The same individuals were exposed to all water velocities in trial 1, and similarly in trial 2, although individuals from trial 1 were not used in trial 2.

ming at a range of speeds; water velocities were largely repeatable among trials (Table 1). Detailed velocity measurements were made every 2 m along the flume length for each combination of trial and treatment, although only measurements taken in the centre of the flume length are reported (Table 1) because they were representative for all locations. Cross-sectional velocity measurements were recorded every 0.2 of flume width and every 0.25 of total depth for medium and fast treatments, and 0.3 of total depth for slow treatments, with water velocity measured using a two-directional electromagnetic velocity meter (model 523; Marsh-McBirney, Loveland USA). An automated passive integrated transponder (PIT) system was used to record the position of fish swimming up the length of the flume (see Castro-Santos et al. 1996, 2013). Ten PIT antennas were mounted along the length of the flume at 2.0 m intervals (from 0.5 to 18.5 m) and a control computer logged tag detection data (tag code, date, time to the nearest 0.1 s, and antenna location) from PIT readers at a rate of 10 Hz.

Twenty-two captive *A. fulvescens* were used for swimming trials and these were Wolf River, Wisconsin, USA, stock obtained in 1993 as cultured 2-year-old juveniles and thereafter housed at the S.O. Conte Anadromous Fish Research Center. All individuals had previously been fitted with PIT tags (32 mm \times 3.85 mm half duplex tags; Texas Instruments, Dallas, Texas, USA) via intracoelomic implantation for individual identification. Prior to tagging with accelerometers, individuals were measured and weighed and subsequently immobilized for the tagging procedure using electrical narcosis (30 VDC impressed voltage; Henyey et al. 2002). Each individual was fitted with a tri-axial accelerometer data-storage tag mounted externally at the base of the dorsal fin (Figs. 1a–1c). Accelerometers were attached by passing a single piece of 18-gauge stainless-steel wire through a hole at each end of the tag, or affixing wire to the tag temporarily with electrical tape. The wire was passed through a neoprene pad to prevent abrasion and then through two hypodermic needles passed through the dorsal musculature of the fish. Following removal of the needles, an additional neoprene pad was added followed by a 5 mm thick

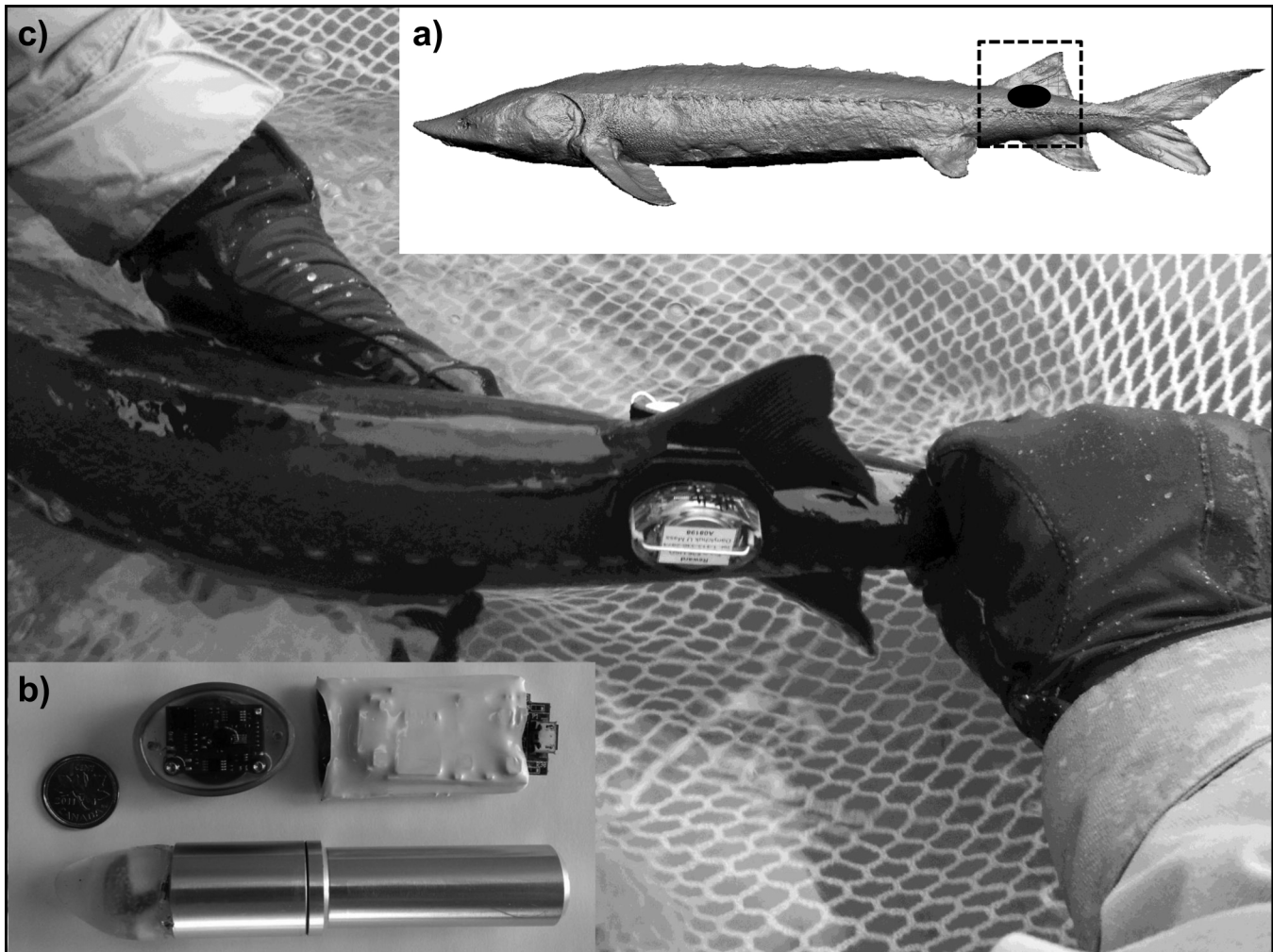
plastic backing plate with predrilled holes. Tags were secured by creating two separate 90° bends in each end of the wire to lock it onto the outside of the backing plate.

Three types of tri-axial accelerometer data-storage tags were used in this study to maximize sample sizes and this enabled evaluation of the strengths and weaknesses of different designs to inform future studies. Tags are hereafter referred to as tag type 1 (model G6a, 40 mm \times 28 mm \times 16.3 mm, 18.5 g in air, 8-bit resolution; CEFAS Technology LTD, Suffolk, UK), type 2 (model X6-2, 52 mm \times 28 mm \times 8 mm, 20 g in air, 12-bit resolution; Gulf Coast Data Concepts, LLC, Waveland, Mississippi, USA), and type 3 (daily diary, 120 mm \times 25 mm, 63 g in air, 22-bit resolution; Wilson et al. 2008), respectively. Tags were programmed to record acceleration in units of gravity (g), equivalent to 9.8 m·s⁻², in separate x , y , and z planes (measurement range: $\pm 2g$) at user-defined intervals of 20 Hz (tag types 1 and 3) or 25 Hz (tag type 2). Device output was calibrated by rotating the device through known angles to real g (Gleiss et al. 2010). Accelerometers were attached on 26 September 2011 ($n = 7$) and on 26 October 2011 ($n = 15$). Immediately following tag attachment, *A. fulvescens* were released into the flume staging area where they were able to ascend the flume volitionally from a low-velocity staging area over ~ 20 h at each of the three water-velocity treatments over a 3-day period. Trial 1 began at the medium-velocity treatment (1.00 m·s⁻¹), followed by the slow treatment (0.48 m·s⁻¹) and then the fast treatment (1.36 m·s⁻¹). Trial 2 began at the slow-velocity treatment (0.48 m·s⁻¹), followed by the fast treatment (1.38 m·s⁻¹) and then the medium treatment (0.99 m·s⁻¹). Following cessation of trials, individuals were recaptured, external tag packages removed to enable downloading of data, and the time difference between individual accelerometers and the independent PIT system noted for later time synchronisation. Water temperatures for trials 1 and 2 were 20.05 \pm 0.03 and 10.39 \pm 0.07 °C, respectively.

Data analyses

Accelerometer output was divided into static and dynamic acceleration components using a weighted smoothing interval of

Fig. 1. (a) Attachment location for accelerometers mounted at the base of the dorsal fin on a lake sturgeon (*Acipenser fulvescens*); (b) the three accelerometers used in this study (clockwise from top left): tag types 1, 2, and 3 compared with a Canadian one-cent coin (19 mm diameter); and (c) tag type 1 attached to a lake sturgeon prior to deployment.



1.5 s (Shepard et al. 2008), where the static component represents the gravitational acceleration acting on the tag and the dynamic component is a function of device movement imparted via muscular contraction (Gleiss et al. 2011). Smoothed acceleration values in each axis were subtracted from raw acceleration to yield the dynamic component (Fig. 2a). Four activity metrics were derived from dynamic acceleration: ODBA (g) and VeDBA (g) (Fig. 2b), as well as TBF (Hz) and TBAA (g) (Fig. 2c). Both ODBA and VeDBA represent single, integrated measures of body motion in all three spatial dimensions; instantaneous (20 Hz) ODBA values were obtained by summing the absolute values of dynamic acceleration in all three axes (Wilson et al. 2006; Gleiss et al. 2011):

$$(1) \quad \text{ODBA} = |A_x| + |A_y| + |A_z|$$

where A_x , A_y , and A_z represent the dynamic acceleration components of the three orthogonal axes of the accelerometer. The vectorial sum (VeDBA; Qasem et al. 2012) is calculated as

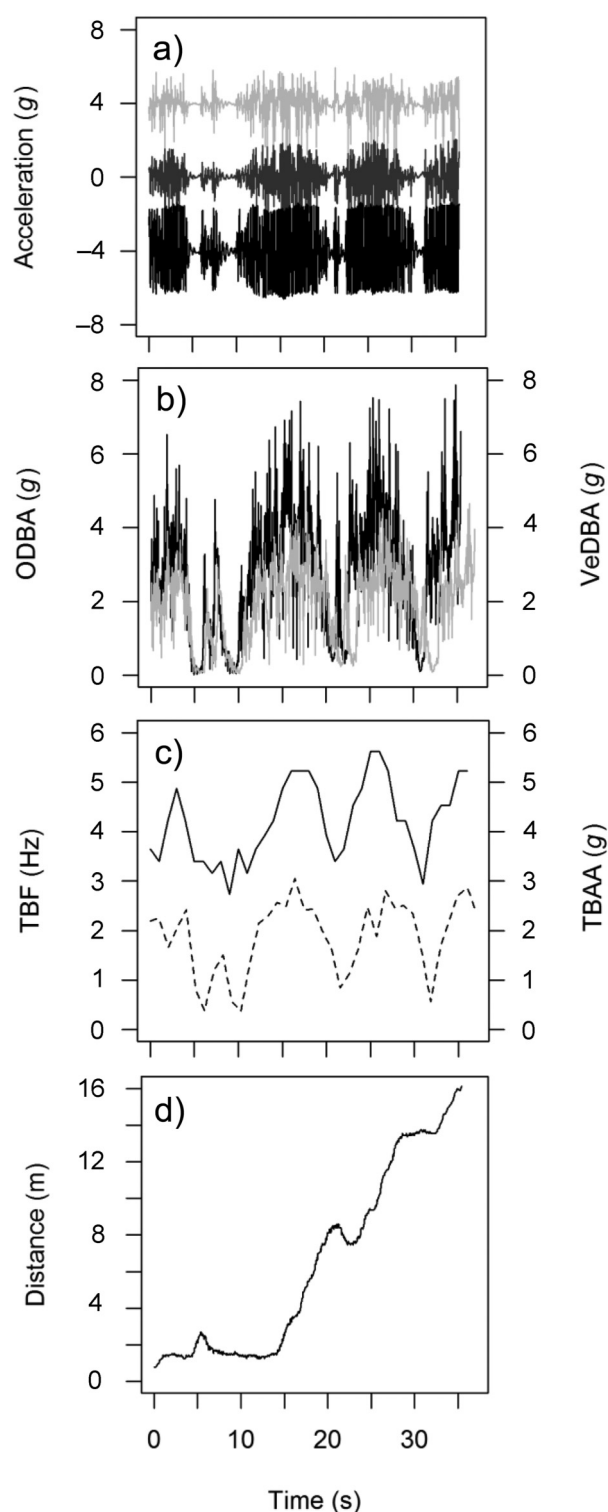
$$(2) \quad \text{VeDBA} = \sqrt{(A_x^2 + A_y^2 + A_z^2)}$$

Tail-beat frequency and TBAA were derived from the dynamic acceleration component of the sway (A_z) axis and represent dy-

namic motion through body and caudal-fin oscillations. Use of the term amplitude does not refer directly to TBA, but rather to the amplitude of the signal derived from the accelerometer through motion of the body and caudal fin during swimming (Whitney et al. 2010). An acceleration spectrogram was first created using continuous wavelet transformation with the Morlet wavelet function (using a nondimensional frequency parameter of 8) in the Ethographer extension (Sakamoto et al. 2009; available from <http://bre.soc.i.kyoto-u.ac.jp/bls/index.php?Ethographer>, accessed 12 September 2012) in Igor Pro version 6.0 (WaveMetrics Inc., Lake Oswego, Oregon, USA). The peak-tracer option in Ethographer was subsequently used to determine the dominant frequency and amplitude of the fitted wavelet, resulting in TBF and TBAA values for every second of sway acceleration. Validation of TBF was performed on a subset of data at each nominal water velocity by undertaking manual counts of TBF on the relevant dynamic acceleration axis and confirmed the accuracy of the peak-tracer method.

Initial attempts to pair instantaneous U_s estimates with corresponding accelerometer-derived metrics (TBF, TBAA, ODBA, and VeDBA) failed because of slight time offsets between the PIT system and some accelerometers. Subsequently, a single U_s estimate was generated for each individual at a nominal velocity, if volitional ascent occurred, and the first full ascent of the flume (typically this was the first attempt) was used in this calculation and paired with mean corresponding TBF, TBAA, ODBA, and VeDBA

Fig. 2. Acceleration profile of a lake sturgeon (*Acipenser fulvescens*) (95 cm total length) during ascension of a 18 m open channel flume swimming against 1.38 m·s⁻¹ water velocity, represented by (a) the dynamic component of acceleration presented for separate *x* (light grey), *y* (dark grey), and *z* (black) axes, with a +4*g* and -4*g* added to *x* and *z* axes, respectively, for graphical purposes only; (b) overall dynamic body acceleration (ODBA, black line; derived from the absolute sum of dynamic acceleration in all three axes) and vectorial dynamic body acceleration (VeDBA, grey line; derived from the vectorial sum of dynamic acceleration in all three axes); (c) tail-beat frequency (TBF, solid line) and tail-beat acceleration amplitude (TBAA, broken line), derived from *z* axis (sway) dynamic acceleration; and (d) spatial location within the flume, expressed as distance from flume entry (0 m), with location determined using passive integrated transponder antennas spaced every 2 m.



values over the flume ascent. Continuous detection of an individual occurred on the PIT system resulting in simultaneous records at adjacent antennas. An adjacent averaging smoothing algorithm (i.e., running mean) was subsequently applied to the PIT data set to provide continuous spatial positioning within the flume (e.g., Fig. 2d). Data were removed past antenna 9 (16.5 m) because of increased turbulence beyond this location. The time difference between the first record of a full flume ascent and the time corresponding to the maximum upstream distance (antenna 9) was used in the calculation of ground speed (U_g). Ground speed (m·s⁻¹) was determined by the difference between the adjacent averaged minimum distance (flume entry) and the first record of maximum distance, divided by the corresponding period of time. Swimming speed (U_s ; m·s⁻¹) was calculated by adding the measured water velocity for a given treatment to U_g (after Castro-Santos et al. 2013).

Linear models were fitted to examine whether a predictive relationship could be developed between accelerometer-derived metrics of activity (ODBA, VeDBA, TBF, or TBAA) and swimming speed. The amplitude and frequency of tail beats have previously been demonstrated to scale linearly with U_s in *A. fulvescens* (Webb 1986), and acceleration scales linearly with U_s in other species of fish (e.g., Wilson et al. 2013). Models were fitted separately for each tag type, as the effect of water temperature could not be differentiated from tag type given no overlap between tag types and water temperatures occurred. All U_s values were normalized to body lengths (BL) · s⁻¹, although individual lengths of *A. fulvescens* were included as an interaction term in the model selection process to determine if length-specific influences on swimming kinematics were evident (Webb 1986). Given that multiple data points were collected for some individuals (maximum of three when an individual ascended the flume at each velocity treatment) potentially violating the assumption of independence for the statistical treatments, linear mixed-effect (LME) models were initially identified as the appropriate approach to examine predictive relationships. To assess the need for a mixed-modelling approach, full models (i.e., all predictors) including random intercept, random slope, or random intercept and slope combinations were compared, using Akaike's information criterion (AIC), with a model having the same predictors but no random effects (Zuur et al. 2009). This comparison was done using package nlme (Pinheiro et al. 2012) in R version 2.14.2 (R Development Core Team 2012) and revealed that the use of a LME model did not result in improved model fit. Subsequently, models without random effects (i.e., ordinary multiple regression) were used for all further analyses.

Two alternative models were fitted for each tag type and accelerometer-derived metric. Models included either accelerometer-derived metrics alone or an interaction with total length (TL). Model selection and multimodel inference were carried out using AIC adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002) using package AICcmodavg (Mazerolle 2012). According to this criterion, the model with the lowest AIC_c value is the most

parsimonious one describing the data and models with a Δ_i (representing the difference in AIC_c scores relative to the top model) of <2, 4–7, and >10 are regarded as having substantial, considerably less, and essentially no support from the data, respectively (Burnham and Anderson 2002). The AIC_c weight (w_i) of the models was also determined and represents the probability of a given model in the set being the most parsimonious one to describe the data (Burnham and Anderson 2002). To account for model selection uncertainty, model-averaged estimates and unconditional 95% confidence intervals were computed using the scaled w_i of the

models included in a 95% confidence set (cumulative weight) for the best model where relevant (Burnham and Anderson 2002). Residuals were examined visually for normality and homogeneity of variance.

Results

Acipenser fulvescens volitionally entered and ascended the flume during both trials and at all three water-velocity treatments. Tag failure (tag type 3 only) occurred on six occasions for unknown reasons, resulting in loss of data for an entire trial or missing data for a water-velocity treatment. In addition, some individuals did not ascend the flume during any treatment ($n = 3$), although more frequently individuals ascended during one treatment and not others. Final sample size consisted of 26 ascents paired with acceleration data, comprising 16 individuals (Table 1). Total length ranged 81–98 cm (90 ± 1 cm TL, mean \pm SE). Volitional U_s ranged 0.48–2.70 $\text{m}\cdot\text{s}^{-1}$ or 0.51–3.18 $\text{BL}\cdot\text{s}^{-1}$. Associated accelerometer-derived activity metrics ranged 0.43–5.79 Hz for TBF, 0.04g–2.45g for TBAA, 0.06g–3.96g for ODBA, and 0.06g–2.57g for VeDBA.

All accelerometer-derived metrics were linearly related to U_s in this study, and predictive relationships were strong with coefficients of determination ranging 0.89–0.97 for the top-ranked models (Table 2). There was substantial support for the inclusion of accelerometer-derived metrics alone in all models and considerably less support for the inclusion of an interaction between TL and TBF, TL and ODBA, and TL and VeDBA for tag type 1 only (Table 2). There was essentially no support for the inclusion of an interaction term between TL and any accelerometer-derived metrics for other tag types (Table 2). The relationship between accelerometer-derived metrics and U_s ($\text{BL}\cdot\text{s}^{-1}$) could be generally approximated by the following equations when combining tag types (Figs. 3a–3d):

$$(3) \quad U_s = 0.4575 \times \text{TBF} + 0.2073$$

$$(4) \quad U_s = 0.9407 \times \text{TBAA} + 0.6354$$

$$(5) \quad U_s = 0.6106 \times \text{ODBA} + 0.6276$$

$$(6) \quad U_s = 0.9398 \times \text{VeDBA} + 0.5900$$

although parameter estimates varied among tag types (Table 3). Swimming speed increased variably 0.45–0.49 $\text{BL}\cdot\text{s}^{-1}$ for every 1 Hz increase in TBF, depending on tag type, and 0.90–1.43, 0.54–0.76, and 0.84–1.19 $\text{BL}\cdot\text{s}^{-1}$ for every 1g increase in TBAA, ODBA, and VeDBA, respectively (Table 3).

Discussion

All four accelerometer-derived metrics of activity used in this study accurately predicted U_s by linear relationship and thus provide a useful tool for the field measurement of activity in *A. fulvescens*. Furthermore, use of a large open channel flume to obtain volitional U_s elicited a wider range of speeds than would be expected from use of a swim tunnel and more likely represents the range of U_s attained by free-swimming *A. fulvescens*. When using confined swim tunnels, it is notoriously difficult to generate U_s data for acipenserids, as they frequently exhibit station holding (i.e., contact with the benthos) when forced to swim at high water velocities; a behavioural strategy that enables them to occupy high-velocity areas while minimizing energy expenditure (Adams et al. 2003; Geist et al. 2005). Subsequently, techniques including prodding (Peake et al. 1997; Adams et al. 2003) or training (McKinley and Power 1992; Geist et al. 2005) are often necessary to induce swimming. Interestingly, the U_s observed in this study are above the upper limits of those previously identified for this species (maximum 1.80 $\text{m}\cdot\text{s}^{-1}$ during endurance tests; Peake et al. 1997). This particular result is consistent with recent findings for

Table 2. Multiple regression models describing lake sturgeon (*Acipenser fulvescens*) swimming speed (U_s ; body lengths (BL) $\cdot\text{s}^{-1}$) in relation to activity metrics (tail-beat frequency (TBF), tail-beat acceleration amplitude (TBAA), overall dynamic body acceleration (ODBA), and vectorial dynamic body acceleration (VeDBA)) derived from data-storage accelerometer tags and total length (TL) of individual fish.

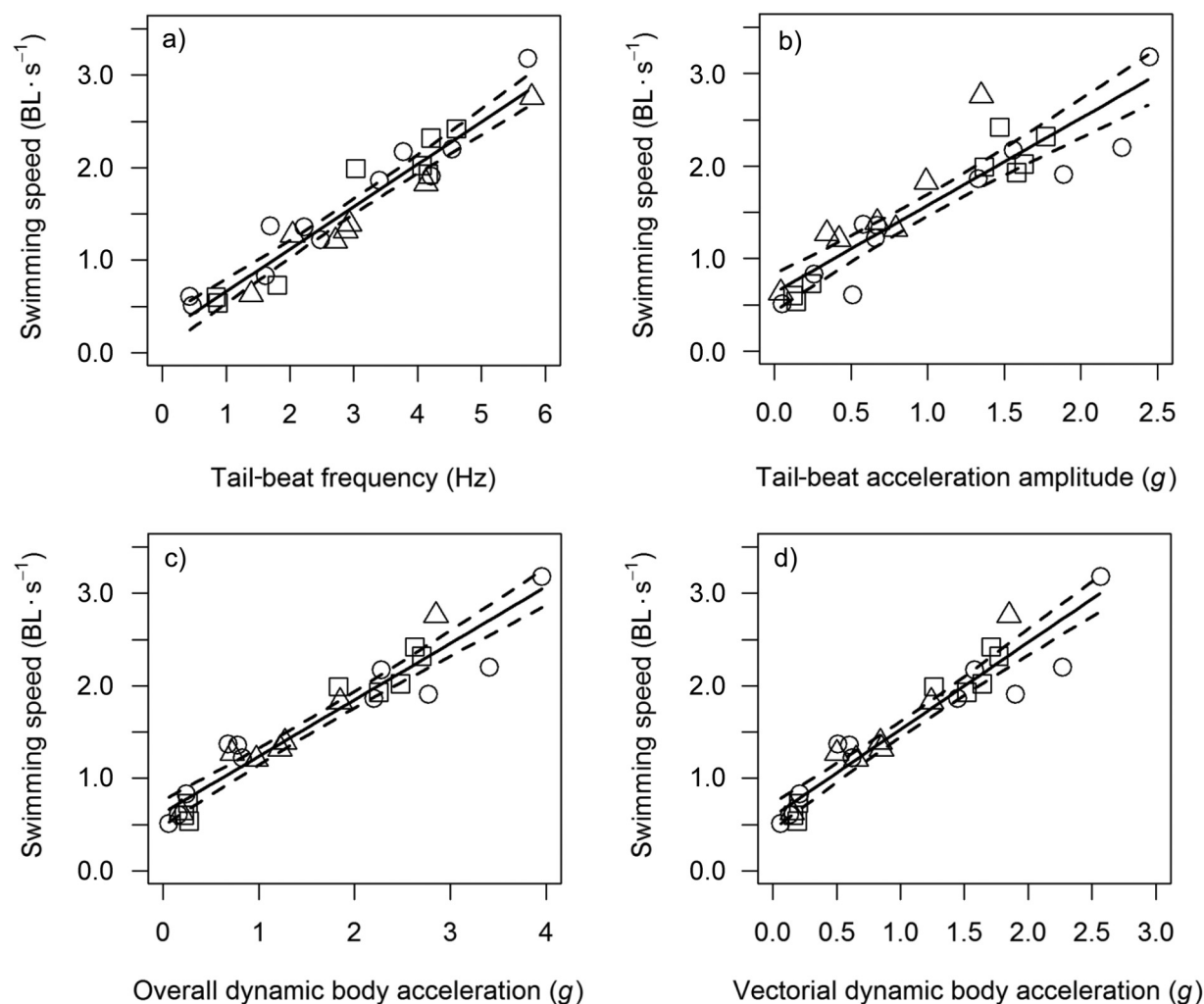
Metric	Tag		AIC _c	Δ_i	w_i	K	Adjusted R ²
	type	Model					
TBF	1	$U_s \sim \text{TBF}$	4.54	0.00	0.91	3	0.93
		$U_s \sim \text{TBF} \times \text{TL}$	9.23	4.69	0.09	5	0.95
	2	$U_s \sim \text{TBF}$	8.71	0.00	1.00	3	0.92
		$U_s \sim \text{TBF} \times \text{TL}$	19.71	11.00	0.00	5	0.99
		$U_s \sim \text{TBF}$	4.64	0.00	1.00	3	0.95
		$U_s \sim \text{TBF} \times \text{TL}$	34.35	29.70	0.00	5	0.99
TBAA	1	$U_s \sim \text{TBAA}$	12.01	0.00	0.98	3	0.86
		$U_s \sim \text{TBAA} \times \text{TL}$	20.23	8.22	0.02	5	0.88
	2	$U_s \sim \text{TBAA}$	6.74	0.00	1.00	3	0.94
		$U_s \sim \text{TBAA} \times \text{TL}$	33.36	26.63	0.00	5	0.92
		$U_s \sim \text{TBAA}$	11.78	0.00	1.00	3	0.86
		$U_s \sim \text{TBAA} \times \text{TL}$	64.87	53.09	0.00	5	0.85
ODBA	1	$U_s \sim \text{ODBA}$	8.74	0.00	0.97	3	0.89
		$U_s \sim \text{ODBA} \times \text{TL}$	15.70	6.96	0.03	5	0.92
	2	$U_s \sim \text{ODBA}$	2.27	0.00	1.00	3	0.96
		$U_s \sim \text{ODBA} \times \text{TL}$	25.87	23.61	0.00	5	0.97
		$U_s \sim \text{ODBA}$	2.76	0.00	1.00	3	0.96
		$U_s \sim \text{ODBA} \times \text{TL}$	45.53	42.77	0.00	5	0.99
VeDBA	1	$U_s \sim \text{VeDBA}$	8.71	0.00	0.96	3	0.89
		$U_s \sim \text{VeDBA} \times \text{TL}$	14.94	6.23	0.04	5	0.92
	2	$U_s \sim \text{VeDBA}$	1.70	0.00	1.00	3	0.97
		$U_s \sim \text{VeDBA} \times \text{TL}$	24.98	23.28	0.00	5	0.97
		$U_s \sim \text{VeDBA}$	3.78	0.00	1.00	3	0.96
		$U_s \sim \text{VeDBA} \times \text{TL}$	49.96	46.17	0.00	5	0.98

Note: Models are fitted separately for three different accelerometer tag types. Candidate models are ranked based on Akaike weight (w_i), which is equivalent to the relative importance of the model. AIC_c, Akaike's information criterion corrected for small sample size; Δ_i , difference in AIC_c scores relative to the top model; K, number of estimable parameters; adjusted R², coefficient of determination.

other species when large flumes are used to generate volitional U_s (Tudorache et al. 2007, 2010; Castro-Santos et al. 2013). Using a swim tunnel to generate endurance-fatigue curves for *A. fulvescens*, Peake et al. (1997) predicted that a 120 cm *A. fulvescens* swimming at 14 °C could cover a distance of only ~13 m prior to fatigue at the upper water-velocity treatment used in this study (1.38 $\text{m}\cdot\text{s}^{-1}$). The authors also noted that maximum distance decreased with decreasing fish length and increasing water temperature. That value represents an underestimate based on the findings of the current study. Others have noted high U_s is achievable by acipenserids, which is unsurprising given their large size can equate to relatively high absolute U_s (Peters 1983). For example, Webber et al. (2007) found that larger (135–198 cm) white sturgeon (*Acipenser transmontanus* Richardson, 1836) were able to achieve positive U_g over short distances against high water velocities (2.54 $\text{m}\cdot\text{s}^{-1}$), although the distances that could be achieved at these velocities and the resulting U_s remain unknown.

Tail-beat frequency was the only metric used in the current study for which data from other acipenserids, including *A. fulvescens*, exists for comparison. The U_s -TBF relationship identified by Webb (1986) is largely similar to the results from this study. Webb (1986) swam juvenile *A. fulvescens* (mean 15.7 cm TL) in a swim tunnel and identified that the relationship between U_s and TBF was best described by the equation $\text{TBF} = 0.07 \times U_s + 1.67$. Thus, a 15.7 cm *A. fulvescens* swimming at 3 $\text{BL}\cdot\text{s}^{-1}$ (equivalent to 47.1 $\text{cm}\cdot\text{s}^{-1}$) would result in a TBF of ~5 Hz. The general model describing TBF in this study would result in a slightly lower, although comparable, U_s of 2.5 $\text{BL}\cdot\text{s}^{-1}$ at a TBF of 5 Hz. No information exists with which to compare the other accelerometer-derived metrics of activity with

Fig. 3. Estimates of swimming speed (U_s ; BL is body length) of lake sturgeon (*Acipenser fulvescens*) in relation to (a) tail-beat frequency, (b) tail-beat acceleration amplitude, (c) overall dynamic body acceleration, and (d) vectorial dynamic body acceleration. Models use all tag types combined and individual values for tag types are indicated for tag type 1 (circle), type 2 (square), and type 3 (triangle). Solid lines indicate model estimates and broken lines indicate lower and upper 95% confidence intervals.



U_s of acipenserids, although ODBA, and to a lesser extent VeDBA, have been widely used as an activity metric in other studies on various taxa (see Halsey et al. 2011). The predictive relationships developed in this study are largely reflective of steady swimming by *A. fulvescens* in a low-turbulence environment. Others have suggested that ODBA (and presumably VeDBA) would be a better predictor than TBF of unsteady swimming behaviours, such as those comprising frequent turns and bursting and coasting, as they are more indicative of total work output (Gleiss et al. 2010, 2011). Gleiss et al. (2011) go on to advocate for the use of VeDBA over ODBA given that VeDBA is theoretically more robust to differences in attachment angle than ODBA, although both appear to provide similarly strong predictive relationships when compared (Qasem et al. 2012; this study). Unsurprisingly, the frequency of a signal (i.e., TBF) remains unaffected by tag orientation, although the derivation of both TBF and TBAA, using the methods outlined in this study, are more complex than the simple calculations of ODBA or VeDBA.

The predictive relationships describing specific accelerometer-derived metrics and U_s in *A. fulvescens* varied somewhat among the three tag types used in this study. Given that swimming trials were conducted at two different water temperatures (10 and 20 °C) and there was no overlap in the use of the same tag type between trials, the effect of tag type and temperature could not be distin-

guished and subsequently parameter estimates for models were presented for individual tag types. Water temperature may have contributed to the variability in parameter estimates in this study, as water temperature affects fish swimming kinematics through both changes in the rates of chemical reactions that control muscular contraction (Beamish 1978) and changes in the density and viscosity of water (Fuiman and Batty 1997). Different tag types and their associated physical size may also have affected the drag experienced by *A. fulvescens* and subsequently influenced the relationship between U_s and accelerometer-derived metrics among tag types. Different drag loads have previously been shown to affect U_s -specific swimming kinematics in other species (e.g., rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792); Webb 1971). Given the larger dimensions of tag type 3 in comparison with tag types 1 and 2 used in this study, it appears logical that accelerometer-derived metrics such as ODBA or VeDBA would be higher for the same U_s in larger tags, although this was not the case. It may be that the variability observed was simply an artefact of the modest sample sizes used in the current study.

The use of an open channel flume to estimate volitional U_s in the current study precluded development of predictive relationships between accelerometer-derived metrics of activity and Mo_2 for *A. fulvescens*. A previous study of similarly sized *A. fulvescens* by McKinley and Power (1992) indicated a linear U_s - Mo_2 relationship

Table 3. Parameter estimates and 95% confidence intervals (CI) explaining lake sturgeon (*Acipenser fulvescens*) swimming speed (U_s ; body lengths (BL) · s⁻¹) in relation to activity metrics (tail-beat frequency (TBF), tail-beat acceleration amplitude (TBAA), overall dynamic body acceleration (ODBA), and vectorial dynamic body acceleration (VeDBA)) derived from data-storage accelerometer tags and total length (TL) of individual fish.

Tag type	Variable	Parameter estimate	95% CI	
			Lower	Upper
1	Intercept	0.2332	-0.8386	1.3050
	TBF	0.4520	0.3741	0.5299
	TBF:TL	-0.0012	-0.0024	0.0001
2	Intercept	0.1304	-0.5950	0.8559
	TBF	0.4937	0.3861	0.6012
3	Intercept	0.0875	-0.1886	0.3635
	TBF	0.4482	0.3671	0.5293
1	Intercept	0.5686	0.2620	0.8752
	TBAA	0.8966	0.6719	1.1213
2	Intercept	0.4624	0.2090	0.7158
	TBAA	1.0638	0.8607	1.2670
3	Intercept	0.5492	0.2040	0.8944
	TBAA	1.4273	0.9800	1.8746
1	Intercept	0.7072	0.4692	0.9451
	ODBA	0.5435	0.4283	0.6588
2	Intercept	0.4679	0.2781	0.6578
	ODBA	0.6967	0.5973	0.7961
3	Intercept	0.4993	0.3171	0.6815
	ODBA	0.7624	0.6424	0.8824
1	Intercept	0.6579	0.4123	0.9035
	VeDBA	0.8389	0.6613	1.0165
2	Intercept	0.4389	0.2525	0.6254
	VeDBA	1.0696	0.9225	1.2168
3	Intercept	0.4563	0.2537	0.6589
	VeDBA	1.1869	0.9854	1.3883

Note: Models are fitted separately for three different accelerometer tag types. Estimates for tail-beat frequency in tag type 1 were computed using the scaled AIC_c (Akaike's information criterion corrected for small sample size) weight (w_i) of the models included in a 95% confidence set (cumulative weight) for the best model.

across a narrower range of U_s (0.30–0.80 m·s⁻¹). However, Mo_2 may not necessarily increase linearly with U_s across such a broad range of U_s . Swimming speed in teleosts more typically increases with the logarithm of Mo_2 , and at higher U_s , energetic demands transition from being met by aerobic respiration to being met anaerobically (Beamish 1978; Jayne and Lauder 1994). Furthermore, there was some evidence of variability in accelerometer metrics, and presumably U_s , during flume ascent in this study that may be indicative of burst-and-coast swimming behaviour (see Figs. 2a–2d), although the frequency of this behaviour was not quantified and this variability was not incorporated into models. Burst-and-coast swimming can be energetically advantageous, as it prolongs the time before exhaustion (Weihs 1974; Videler and Weihs 1982; Tudorache et al. 2007). At moderate and high speeds, burst-and-coast swimming can involve recruitment of anaerobic white muscle fibres (Jayne and Lauder 1994), resulting in glycogen depletion and lactate accumulation (Peake and Farrell 2004). Incorporating finer temporal information on U_s and accelerometer-derived metrics demonstrates promise to elucidate gait transitions and represents an area requiring further research. Although, until new U_s – Mo_2 relationships are established, across a broad range of field-relevant U_s , the activity-specific costs of these behaviours remain theoretical. Furthermore, the limitations imposed by the physical size of some animals, including for adults of many members of the Acipenseridae, and the resulting difficulties of constructing

large swim tunnels or respirometers, indicate that extrapolation or borrowing from similar species (e.g., Semmens et al. 2013) is currently necessary.

This study is in agreement with the growing body of evidence supporting animal-borne accelerometers as a useful tool for the derivation of activity and energy expenditure across a broad range of aquatic and terrestrial taxa (Halsey et al. 2011; Brown et al. 2013). Furthermore, this type of data can be used in the determination of landscape-dependent energy expenditure and the subsequent construction of energy landscapes (Wilson et al. 2012). Beyond the clear implications of such research (Tomlinson et al. 2014), it is also possible to use sensors such as this to quantify animal responses to different anthropogenic disturbances and infrastructure (Wilson et al. 2015). In the context of fish, acceleration sensors hold particular promise for studying issues related to fish passage (e.g., Burnett et al. 2014; Silva et al. 2015). While the relationships between unsteady swimming and accelerometer-derived metrics of activity remain unknown and represent an important knowledge gap, the utility of accelerometers as a direct measure of volitional U_s in *A. fulvescens* was demonstrated. Extension of this relationship to estimate the energy expenditure of wild *A. fulvescens* in the context of measuring routine activity or potentially energetically demanding activities such as migrations holds promise, although a lack of published data on U_s – Mo_2 requires a number of assumptions and highlights the need for further work.

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