

REGULAR PAPER

Estimating fish swimming metrics and metabolic rates with accelerometers: the influence of sampling frequency

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Accelerometry is growing in popularity for remotely measuring fish swimming metrics, but appropriate sampling frequencies for accurately measuring these metrics are not well studied. This research examined the influence of sampling frequency (1–25 Hz) with tri-axial accelerometer biologgers on estimates of overall dynamic body acceleration (ODBA), tail-beat frequency, swimming speed and metabolic rate of bonefish *Albula vulpes* in a swim-tunnel respirometer and free-swimming in a wetland mesocosm. In the swim tunnel, sampling frequencies of ≥ 5 Hz were sufficient to establish strong relationships between ODBA, swimming speed and metabolic rate. However, in free-swimming bonefish, estimates of metabolic rate were more variable below 10 Hz. Sampling frequencies should be at least twice the maximum tail-beat frequency to estimate this metric effectively, which is generally higher than those required to estimate ODBA, swimming speed and metabolic rate. While optimal sampling frequency probably varies among species due to tail-beat frequency and swimming style, this study provides a reference point with a medium body-sized sub-carangiform teleost fish, enabling researchers to measure these metrics effectively and maximize study duration.

KEYWORDS

accelerometer, *Albula vulpes*, biologging, bonefish, metabolism, swimming speed

1 | INTRODUCTION

Characterizing how animals behave and expend energy in the wild in relation to ecological factors and anthropogenic stressors plays an important role in both fundamental biology and applied conservation (Buchholz, 2007; Cooke *et al.*, 2014; Sutherland, 1998). Historically, fish expenditure was typically estimated in relation to swimming speed and tail-beat frequency in laboratory settings due to the conveniences of quantifying these metrics with cameras (Bainbridge, 1958; Krohn and Boisdair, 1994). Recent advances in biologging and biotelemetry technologies are now enabling unprecedented insight into animal behaviour and bioenergetics in natural environments (Cooke *et al.*, 2016; Hussey *et al.*, 2015; Wilmers *et al.*, 2015). Accelerometer tags (transmitters or biologgers) are being increasingly employed to measure animal behaviour and energetics both in the wild and in captivity (see Brown *et al.*, 2013; Cooke *et al.*, 2016). Tri-axial accelerometers are most commonly used, which quantify both animal movement (dynamic acceleration) and body posture (static acceleration due to gravity) in three dimensions. This is useful for quantifying

activity levels (Gleiss *et al.*, 2011), as well as finer scale behaviours including individual strides, fin or wing beats, or more general behaviours such as mating or foraging (Brown *et al.*, 2013). With appropriate respirometric calibrations, accelerometers can also be used to estimate the active metabolism of animals based on movement (Gleiss *et al.*, 2011; King *et al.*, 2004; Wilson *et al.*, 2006). In particular, overall dynamic body acceleration (ODBA) is a highly consistent proxy for movement speed and metabolic rate (Brownscombe *et al.* 2014; Gleiss *et al.* 2011; Halsey *et al.* 2009; Wright *et al.* 2014). Given that active metabolism represents a major component of a fish's energy budget (Boisclair & Leggett, 1989; Jobling, 1994) and can be highly variable in the wild due to environmental factors, it is a valuable metric for understanding fish ecology and deriving estimates for bioenergetics models (Brodie *et al.*, 2016; Brownscombe *et al.*, 2017).

To capture the range of motion exhibited by animals, accelerometers are typically programmed to sample data multiple times s^{-1} in all three axes (note that it is also possible to sample only 1 or 2 axes but this limits ability to detect a full range of activities). A review of animal accelerometry across all taxa by Brown *et al.* (2013) identified the

most common sampling frequencies cited in ecological literature to be 10, 16 and 32 Hz, but devices can have the capacity to measure up to 300 Hz (Broell *et al.*, 2013). In previous applications in fish, the majority of sampling frequencies ranged from 5 to 25 Hz (Brownscombe *et al.*, 2014, 2017; Tsuda *et al.*, 2006; O'Toole *et al.*, 2010; Whitney *et al.*, 2010; Wilson *et al.*, 2013; Wright *et al.*, 2014). While electing for higher sampling frequencies provides greater temporal resolution and more dependable measures of behaviour and energy expenditure, it also limits tag battery life. To some extent this can be offset by increasing battery size, but this also increases tag burden and restricts the applications of the tag to only larger animals (Jepsen *et al.*, 2005). Another consequence of high frequency sampling is that it can result in excessive data beyond what are necessary to address the research question, complicating analysis and increasing computation times. Identifying optimal sampling frequencies for specific research questions is therefore highly relevant to developing best practices for accelerometry.

Accelerometer tags have been applied to diverse fish species to address a range of fundamental and applied research questions, from general activity to fine scale behaviours and energetics (Broell *et al.*, 2013; Brownscombe *et al.*, 2013, 2014, 2017; Gleiss *et al.*, 2010; Murchie *et al.*, 2011; O'Toole *et al.*, 2010; Tsuda *et al.*, 2006; Whitney *et al.*, 2007, 2010). Oscillations in sway-axis acceleration are also a reliable proxy for tail-beat frequencies (Brownscombe *et al.*, 2013; Sakamoto *et al.*, 2009), which are metrics that historically have been used as a proxy for metabolic rates (Steinhausen *et al.*, 2005;

Ohlberger *et al.*, 2007). While accelerometers are being increasingly applied to study fish behaviour and energetics, few studies have identified optimal sampling frequencies to capture metrics of interest [but see Halsey *et al.*, (2009) for an example with birds]. Broell *et al.*, (2013) examined the influence of sampling frequency on identifying fine scale behaviours of great sculpin *Myoxocephalus polyacanthocephalus* (Pallas 1814), including feeding strikes and escape events. The authors generally advocated for relatively high frequencies (> 30 Hz) for identification of these fine-scale behaviours. Optimal sampling frequencies for estimating other metrics such as general activity levels, tail-beat frequencies, swimming speeds and metabolic rates are still unclear.

This study aimed to identify optimal accelerometer sampling frequencies for measuring swimming metrics and metabolic rates with a tropical marine teleost fish, the bonefish *Albula vulpes* (L. 1758). Firstly, the influence of sampling rate (1–25 Hz) on estimates ODBA, fish swimming speeds and metabolic rates in a swim-tunnel respirometer were examined. Secondly, variation in estimates of these metrics due to sampling frequency was measured with free-swimming *A. vulpes* in a wetland mesocosm.

2 | MATERIALS AND METHODS

2.1 | Fish capture and holding

Albula vulpes in both experiments described below were captured from Kemps Creek, Eleuthera, The Bahamas, using a seine net and then transported by boat to the wet laboratory facility at the Cape Eleuthera Institute (as per methods described in Murchie *et al.*, 2009). *Albula vulpes* were held at the facility in circular holding tanks (3.7 m diameter × 1.25 m height; 13,180 l) prior to experimentation and were fed daily rations of chopped fish to satiation. All experiments were conducted in accordance with the Canadian Council on Animal Care as administered by the Carleton University Animal Care Committee (Protocol B10-06).

2.2 | Swim tunnel experiment

Swim-tunnel experiments took place between 0700 and 1000 h from 18 to January 27, 2013. The night prior to experimentation, *A. vulpes* ($n = 8$; 48 ± 2.5 cm fork length, L_F ; 35–44 cm range) were tagged with tri-axial accelerometers (model X8M-3, 500 mAh battery, 15 g in air, 25 Hz recording frequency; Gulf Coast Data Concepts; www.gcdataconcepts.com), secured to the *A. vulpes* externally through the dorsal musculature to frontal and backing plates with 36 kg breaking strength braided Dacron line (Figure 1; Brownscombe *et al.* 2014). *Albula vulpes* were fasted for 24 h prior to swim-tunnel experiments and water temperature was consistent during this period ($23.3 \pm 0.9^\circ\text{C}$ s.d.). After tagging, *A. vulpes* were placed into a Blazka-style recirculation swim tunnel (24.1 cm internal diameter × 116 cm length, 2.1 m s^{-1} maximum flow rate; Nowell *et al.*, 2015) to acclimate over night.

In the swim tunnel, *A. vulpes* were subjected to a modified ramp- U_{crit} procedure (Jain *et al.*, 1997) involving increases in water speed in 15 cm s^{-1} increments every 15 min until exhaustion (as per Nowell

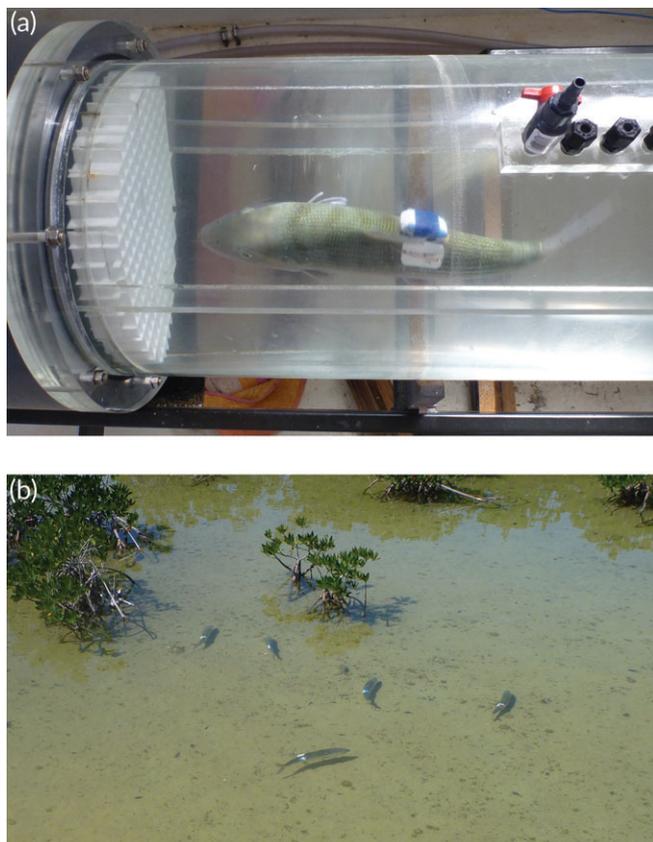


FIGURE 1 Photos of *Albula vulpes* tagged externally with a tri-axial accelerometer bilogger (a) in a swim-tunnel respirometer and (b) swimming in a semi-natural wetland

et al., 2015). At each speed, water oxygen concentrations were measured over a 10 min period using an OxyGuard oxygen probe (OxyGuard Handy Polaris 2, portable DO meter, Water Management Technologies, Inc.; www.w-m-t.com). The swim tunnel was then flushed with fresh seawater directly from the ocean for a 5 min period prior to increasing the water flow speed. Acceleration data at each swimming speed were derived from a minimum of a 1 min period when fish were visually observed maintaining position in the swim tunnel (*i.e.* not falling back nor gaining position within the tunnel). This approach may have incurred some biases due to variation in fish movement throughout the entire 10 min respirometry period that was not captured with the 1 min acceleration measurement period, yet yielded a more accurate estimate of the relationship between acceleration and swimming speed. After experimentation, accelerometers were removed and fish were measured for body mass, total length (L_T), L_F , W_B and D_B for calculations of blocking effect and metabolic rate. Fish were then placed into a holding tank for 24 h prior to release.

Measurements of water oxygen concentration in the swim tunnel were used to estimate *A. vulpes* oxygen consumption rate ($\dot{M}O_2$; mg O_2 min^{-1} kg^{-1}) at each swimming speed using: $\dot{M}O_2 = \Delta[O_2] v (Mt)^{-1}$, where $\Delta[O_2]$ is the change on oxygen concentration (mg l^{-1}), v is the swim tunnel volume (total volume minus the fish's volume; L), M is the fish's mass (kg) and t is time (min). *Albula vulpes* swimming speeds (SS) were corrected for the solid blocking effect (*i.e.*, the increase in water velocity around the fish due to its presence in the tunnel) based on Bell & Terhune (1970): $SS = V \{1 + \{0.4L_F [0.5(M + D_B)]^{-1}\}\} [0.25 \pi D_B M (At)^{-1}]^{1.5}$, where V is swim tunnel water velocity (cm s^{-1}) and A is swim tunnel cross-sectional area.

Tri-axial acceleration data consisted of acceleration (g) in three axes (A_x = surge, A_y = heave, A_z = sway in our fish attachment orientation). These data were subset from the full dataset (25 Hz sampling frequency) to datasets of 1, 3, 5, 10, 15 and 20 Hz. This was accomplished by selecting every n th data row, where $n = (\text{full sampling frequency}) / (\text{subset sampling frequency})^{-1}$. To separate static (gravity) from dynamic (fish movement) acceleration, a box smoother was applied. The optimal smoothing interval was determined using the method described in Shepard *et al.* (2008) for each sampling frequency. While a 2 s running mean was sufficient for sampling frequencies of 3 Hz and higher, a 5 s running mean was applied to the 1 Hz dataset. ODBA (g) was calculated as the absolute sum of the dynamic acceleration in all axes. *Albula vulpes* tail-beat frequency was calculated from A_z -axis dynamic acceleration data using a short-term Fourier transform with the *dfreq* function in the R package *seewave* (Sueur *et al.*, 2008).

Relationships between *A. vulpes* swimming speed, ODBA, tail-beat frequency and metabolic rate in the swim tunnel were fit with a series of linear mixed effects (LMM) models using the package *nlme* in R (Pinheiro *et al.*, 2015). At each sampling frequency, LMMs were fit with ODBA as the response and swimming speed as the predictor, tail-beat frequency as the response and swimming speed as the predictor and O_2 as the response and ODBA as the predictor. All models included fish as a random intercept. In addition, linear models were fit to each individual fish for all of these relationships to compare the

mean and error of explained variance (R^2) amongst sampling frequencies.

2.3 | Wetland mesocosm experiment

Albula vulpes ($n = 8$; mean \pm s.d. $L_T = 38.8 \pm 2.3$ cm, 35–42 cm range) were tagged with tri-axial accelerometer loggers in the same manner as the swim-tunnel experiment and immediately placed in a c. 2,500 m^2 semi-natural wetland mesocosm at the Cape Eleuthera Institute on January 18, 2015. The mesocosm is supplied with seawater from the adjacent wet-lab facility and vegetated with red mangrove *Rhizophora mangle* and black mangrove *Avicennia germinans*. This environment is similar to *A. vulpes* habitats in the mangrove creeks of nearshore Eleuthera, but it is disconnected from the ocean and not influenced by tides. Previous work has shown that *A. vulpes* exhibit a range of typical behaviours in this mesocosm, including regular foraging (Brownscombe *et al.*, 2014; Murchie *et al.*, 2011). The data examined here were derived from a 4 h period, 1300–1700 hours on January 19, 2015.

Albula vulpes wetland acceleration data were analyzed in the same manner as the swim tunnel data and mean ODBA was calculated for each second over the 4 h period. Swimming speeds and oxygen consumption rates were then predicted using the models from the swim tunnel experiment. Mean ODBA, swimming speed and metabolic rate for each individual fish were compared between sampling frequencies by fitting linear mixed effects models to each variable with sampling frequency as a predictor and fish ID as a random intercept. Pairwise comparisons were implemented using the *glht* function in the R package *multcomp* (Hothorn *et al.* 2008) to determine whether there were significant differences between sampling frequencies.

3 | RESULTS

3.1 | Swim tunnel experiment

There was a significant positive relationship between *A. vulpes* swimming speed and ODBA, as well as ODBA and metabolic rate in the swim tunnel at all sampling frequencies (Figure 2(a), (c) and Table 1). However, there was no significant relationship between swimming speed and tail-beat frequency at sampling frequencies of < 10 Hz (Figure 2(b) and Table 1). The relationship between ODBA and swimming speed, as well as ODBA and metabolic rate were both highly consistent at sampling frequencies of ≥ 5 Hz, but more variable at lower frequencies (Figure 3(a), (c) and Table 1). However, tail-beat frequency was more consistent with swimming speed at sampling frequencies of ≥ 10 Hz (Figure 3(b) and Table 1).

3.2 | Wetland mesocosm experiment

Measurements of *A. vulpes* ODBA were very consistent at sampling frequencies ≥ 3 Hz, but 1 Hz was significantly higher than other frequencies (Figure 4(a)). Owing to a combination of higher estimates of ODBA as well as variation in predictive-model coefficients from the swim-tunnel experiment, estimates of *A. vulpes* swimming speeds in the wetland were significantly higher at sampling frequencies of

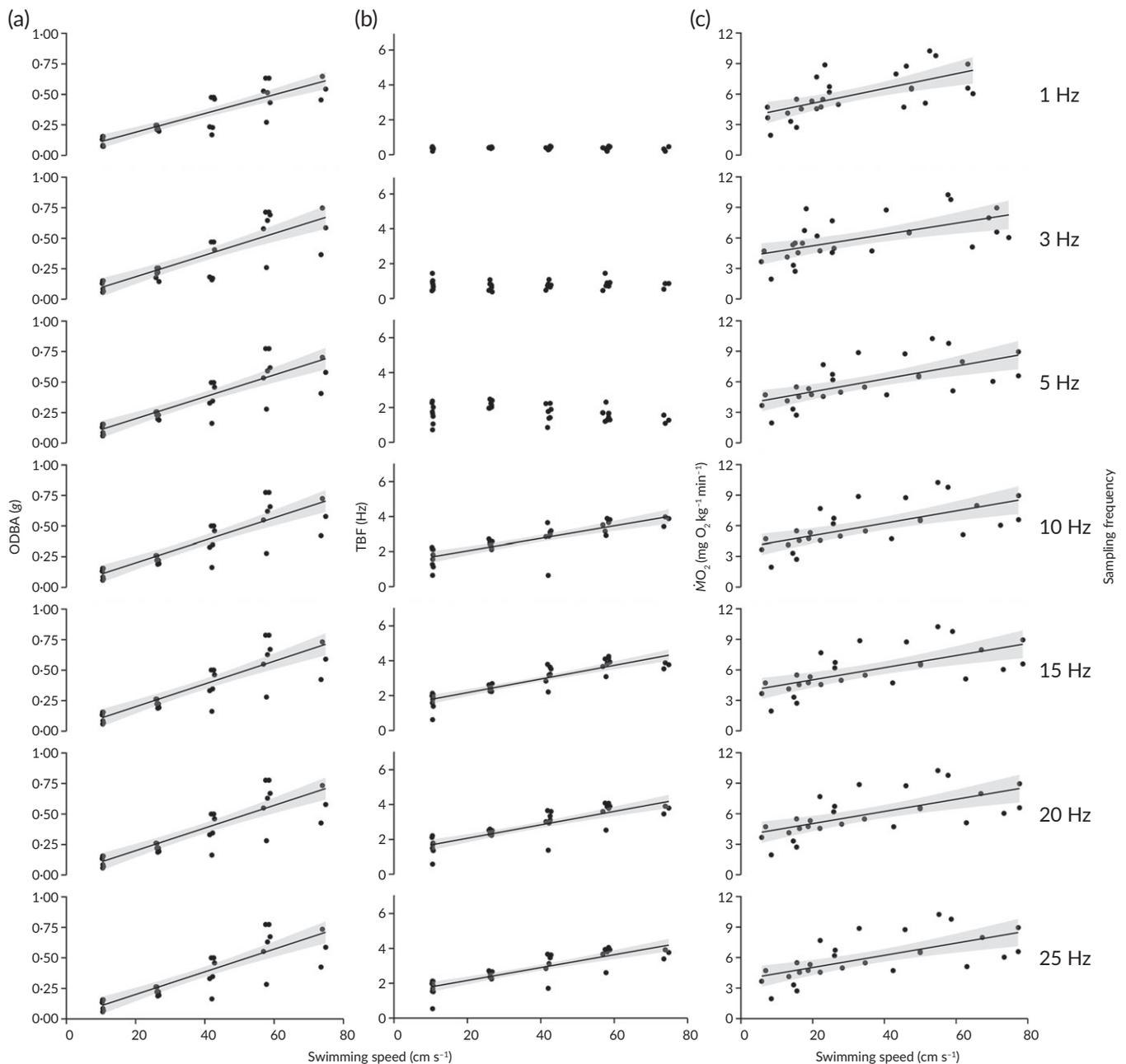


FIGURE 2 The relationship between (a) swimming speed and overall dynamic body acceleration (ODBA), (b) swimming speed and tail beat frequency (TBF), (c) ODBA and metabolic rate at a range of sampling frequencies measured in *Albula vulpes* in a swim-tunnel respirometer. ●, mean value for individual fish at each swimming speed. Where there is a significant relationship, the data were fitted with a linear mixed effect model (■ $\pm 95\%$ c.i.)

< 5 Hz than higher sampling frequencies (Figure 4(b)). Variation amongst sampling frequencies was greatest in estimates of *A. vulpes* metabolic rate, where sampling frequencies of < 10 Hz were significantly different from those 10 Hz or higher (Figure 4(c)).

4 | DISCUSSION

Accelerometry is a valuable tool for studying both animal behaviour and ecological energetics (Brown *et al.*, 2013; Cooke *et al.* 2016). With the rapid expansion in its application, it is important to develop best practices for accelerometry that ensure research questions are addressed effectively. Here we explored the influence of sampling

frequency with tri-axial accelerometers on estimates of ODBA, swimming speeds, tail-beat frequencies and metabolic rates in *A. vulpes*, with the goal of identifying minimum frequencies required to effectively measure metrics that are relevant to fish ecology and bioenergetics. To accomplish this we used a ramp- U_{crit} procedure in a swim-tunnel respirometer (Jain *et al.*, 1997); an important limitation of this approach is that anaerobic recruitment can occur at higher swimming speeds, influencing the estimated relationship between aerobic metabolic rate, acceleration and swimming speed. Importantly, this does not affect our assessment of the influence of accelerometer sampling frequency on estimates of fish swimming metrics because our methods were consistent in both the swim tunnel and free-swimming *A. vulpes* data.

TABLE 1 Linear mixed effects model outputs predicting overall dynamic body acceleration (ODBA) and tail-beat frequency (TBF) by swimming speed, and metabolic rate (MO_2) by ODBA at a range of sampling frequencies with *Albula vulpes* in a swim-tunnel respirometer. Individual was included as a random effect

Model	Frequency (Hz)	Intercept	Value	S.E.	Marginal R^2	Conditional R^2	t	P
ODBA by swimming speed								
1		0.018	0.008	0.0006	0.76	0.87	12.8	<0.001
3		-0.014	0.009	0.0009	0.69	0.82	10.6	<0.001
5		-0.004	0.010	0.0008	0.73	0.87	12.8	<0.001
10		-0.008	0.010	0.0008	0.73	0.87	12.5	<0.001
15		-0.010	0.010	0.0008	0.73	0.86	12.4	<0.001
20		-0.010	0.010	0.0008	0.73	0.86	12.4	<0.001
25		-0.010	0.010	0.0008	0.74	0.87	12.6	<0.001
TBF by swimming speed								
1		0.37	0.0002	0.0005	0.002	0.59	0.3	>0.05
3		0.78	0.0005	0.0020	0.002	0.60	0.3	>0.05
5		1.97	-0.007	0.0040	0.09	0.09	-1.7	>0.05
10		1.23	0.040	0.0040	0.66	0.83	10.6	<0.001
15		1.30	0.040	0.0030	0.78	0.89	14.5	<0.001
20		1.17	0.040	0.0030	0.73	0.91	15.5	<0.001
25		1.30	0.040	0.0030	0.73	0.91	15.4	<0.001
MO_2 by ODBA								
1		3.64	7.25	1.41	0.40	0.62	5.1	<0.001
3		4.07	5.67	1.24	0.36	0.57	4.6	<0.001
5		3.75	6.31	1.19	0.42	0.63	5.3	<0.001
10		3.81	6.07	1.18	0.41	0.62	5.1	<0.001
15		3.82	5.96	1.16	0.40	0.61	5.1	<0.001
20		3.83	5.97	1.17	0.40	0.61	5.1	<0.001
25		3.82	5.99	1.17	0.40	0.61	5.1	<0.001

We found sampling frequencies of just 1 Hz were sufficient to establish strong relationships between ODBA, swimming speed and metabolic rate. However, the variance in these relationships and linear mixed effects model coefficients were more variable below 5 Hz. Further, in free swimming *A. vulpes*, estimates of metabolic rate were significantly different below 10 Hz. Given that higher sampling frequencies are most effective at accurately capturing the full range of animal movement, which is directly related to movement speed and active metabolism, this variation reflects decreased accuracy in estimates of fish swimming speed and metabolic rate at lower sampling frequencies. Similarly, frequencies of < 10 Hz were ineffective at estimating *A. vulpes* tail-beat frequencies in the swim tunnel. Given that the maximum *A. vulpes* tail-beat frequencies observed in the swim tunnel were < 5 Hz, this is consistent with signal processing theory, which suggests sampling must be at least twice as frequent as the highest frequency wave in a waveform (Brown *et al.*, 2013; Yost *et al.*, 1983). Because tail-beat frequencies of free swimming *A. vulpes* reach a maximum of 9 Hz (Brownscombe *et al.*, 2014), sampling frequencies of > 18 Hz would be required to estimate this metric effectively. While estimates of tail-beat frequency from accelerometer tags are valuable for comparisons with previous fish swimming and bioenergetics research (Cooke *et al.*, 2016), higher sampling frequencies are required to acquire accurate estimates of tail-beat frequency than ODBA, swimming speed and metabolism.

While higher sampling frequencies resulted in more accurate estimates of *A. vulpes* swimming speeds and metabolic rates, sampling rates as low as 1 Hz would still provide a measure of general activity level. Conversely, for the measurement of finer scale behaviours, Broell *et al.* (2013) found relatively high sampling frequencies (> 30 Hz) were required to effectively identify rapid feeding strikes and escape responses in *M. polyacanthocephalus*. It is intuitive that rapid behaviours would require higher sampling frequencies to be identified and discriminated. In other work, Brownscombe *et al.* (2014) were able to identify benthic foraging in *A. vulpes* using 25 Hz, whereas Whitney *et al.* (2010) were able to identify nurse shark *Ginglymostoma cirratum* (Bonnaterre 1788) mating behaviours with only 5 Hz sampling frequencies. When choosing a sampling frequency for accelerometer applications, it is important to consider the study objectives and relevant timeframes for metrics of interest.

According to signal processing theory, sampling must be at least twice as frequent as the highest frequency wave in a waveform (Brown *et al.*, 2013; Yost *et al.*, 1983). The sampling frequency will therefore depend to some extent on the species of interest, particularly given the allometric scaling of body movements, with an inverse relationship between animal size and stroke frequency (Sato *et al.*, 2009). In fish, the body shape and swimming style must also be considered because the wavelength of the swimming stroke influences the frequency of the propulsion by tail beat. For example, the short wavelength tail-beat characteristic of fast-swimming thunniform

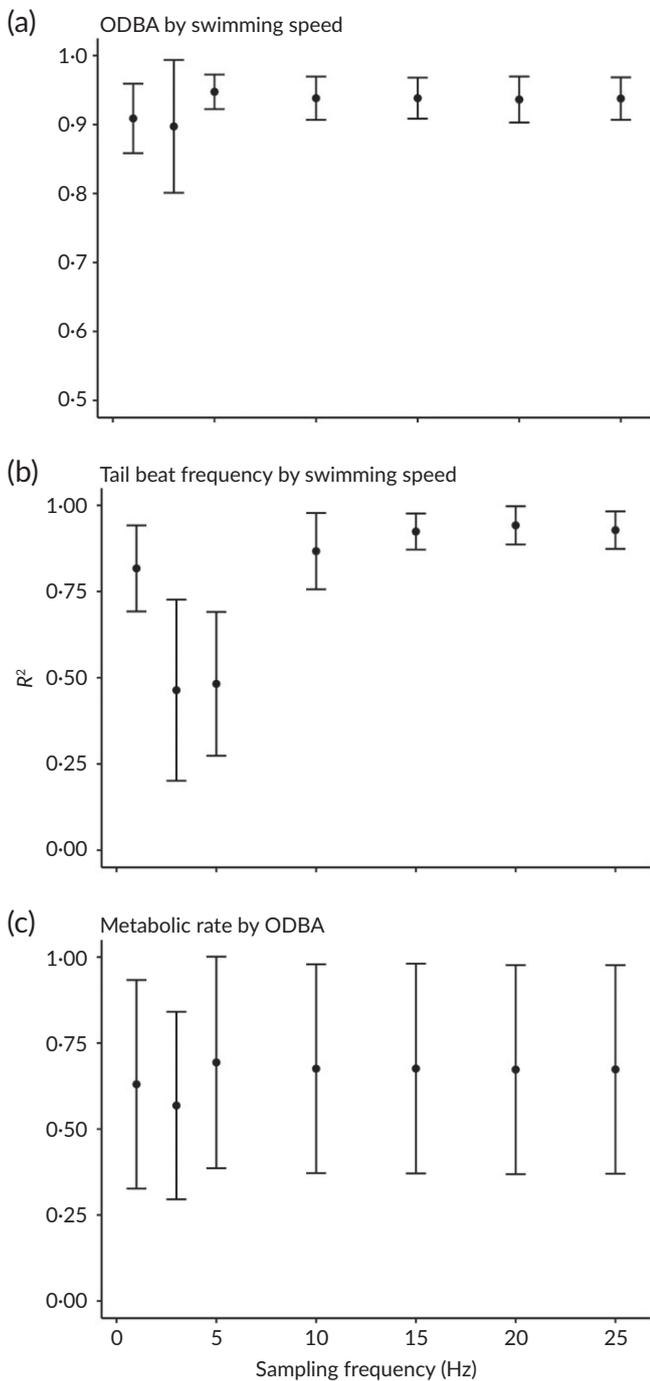


FIGURE 3 Mean (\pm S.E.) explained variance (R^2) in (a) overall dynamic body acceleration (ODBA) by swimming speed, (b) tail-beat frequency by swimming speed, and (c) metabolic rate by ODBA from linear models fit to individual *Albula vulpes* in a swim tunnel

fishes are more frequent than those of slower swimming anguilliform fishes with a longer swimming stroke whose wavelength travels farther down the body [see Froese & Pauly (2016) for swimming styles of fishes]. *Albula vulpes* have a subcarangiform swimming style and our findings suggest that sampling at 10 Hz should suffice for most accelerometer applications unless tail-beat frequency is of interest. Higher frequencies would probably be required for smaller-bodied species, species with shorter movement wavelengths (e.g. thunniform swimmers), or for identifying movements of shorter duration (Broell *et al.*, 2013).

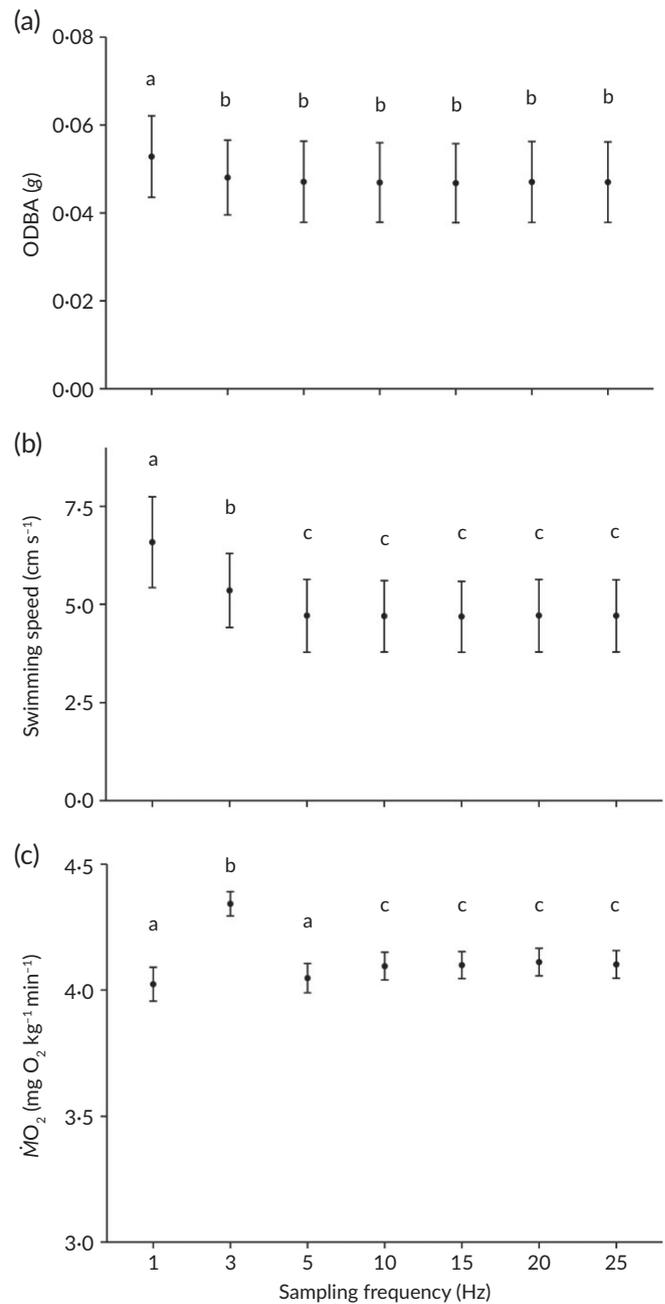


FIGURE 4 Mean (\pm S.E.) estimates of (a) overall dynamic body acceleration (ODBA), (b) swimming speed and (c) metabolic rate from free-swimming *Albula vulpes* in a semi-natural wetland mesocosm over a 4 h period. Different lower-case letters indicate significant differences between sampling frequencies (Tukey's HSD post hoc test, $p < 0.05$) on fitted linear mixed effects models

In recent applications, the majority of studies have employed accelerometer transmitters with relatively low sampling frequencies (typically *c.* 5 Hz; Brownscombe *et al.*, 2017; O'Toole *et al.*, 2010; Payne *et al.*, 2011; Wilson *et al.*, 2013), which should suffice to provide accurate estimates of activity level (ODBA) and swimming speed, although may incur some biases in estimating metabolic rate. Studies employing data loggers generally utilize higher frequencies > 20 Hz that provide greater behavioural resolution, including for measuring tail-beat frequency (Broell *et al.*, 2013; Brownscombe *et al.*, 2013, 2014; Thiem *et al.*, 2015). In some cases, this may be excessively high

if the goal is estimate swimming speed or metabolic rate and not to identify fine scale behaviour or count tail-beat frequencies. There is generally a tradeoff between sampling frequency and study duration, but alternative approaches such as interval sampling can be used to maintain high resolution of data while maintaining a longer period of sampling if necessary (Dow *et al.*, 2009). Advanced onboard processing of acceleration signals to automatic classification of behaviour can also be programmed into tags to limit the onboard memory use (Broell *et al.*, 2013).

In conclusion, accelerometer tags are a valuable tool for remotely measuring fish behaviour and metabolism, with diverse application for understanding how ecological factors influence behaviour and energy expenditure (Brown *et al.*, 2013; Brownscombe *et al.*, 2017; Gleiss *et al.*, 2011), as well as estimates of active metabolic rate for bioenergetics models (Cooke *et al.*, 2016). Identifying the minimum effective sampling frequencies for measuring metrics of interest will ensure that research questions are addressed effectively while also maximizing data collection duration. We found sampling frequencies of ≥ 5 Hz were sufficient to estimate swimming speed from accelerometer-derived ODBA, while ≥ 10 Hz would be most accurate for estimating metabolic rate and higher frequencies are required to estimate tail-beat frequencies (at least twice the maximum TBF). Although lower sampling frequencies provide general estimates of activity levels, higher frequencies are often required to accurately identify finer scale behaviours. Optimal sampling frequencies are certainly related to study objective and metrics of interest, as well as species characteristics, namely body size and swimming style.

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