

## Recent advances in telemetry for estimating the energy metabolism of wild fishes

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Metabolic rate is a critical factor in animal biology and ecology, providing an objective measure that can be used in attributing a cost to different activities and to assessing what animals do against some optimal behaviour. Ideally, metabolic rate would be estimated directly by measuring heat output but, until recently, this has not been easily tractable with fishes so instead metabolic rate is usually estimated using indirect methods. In the laboratory, oxygen consumption rate is the indirect method most frequently used for estimating metabolic rate, but technical requirements preclude the measurement of either heat output or oxygen consumption rate in free-ranging fishes. There are other field methods for estimating metabolic rate that can be used with mammals and birds but, again, these cannot be used with fishes. Here, the use of electronic devices that record body acceleration in three dimensions (accelerometry) is considered. Accelerometry is a comparatively new telemetric method for assessing energy metabolism in animals. Correlations between dynamic body acceleration (DBA) and oxygen consumption rate demonstrate that this will be a useful proxy for estimating activity-specific energy expenditure from fishes in mesocosm or field studies over extended periods where other methods (*e.g.* oxygen consumption rate) are not feasible. DBA therefore has potential as a valuable tool for attributing cost to different activities. This could help in gaining a full picture of how fishes make energy-based trade-offs between different levels of activity when faced with conflicting or competing demands arising from increased and combined environmental stressors.

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### METABOLIC RATE AS A UNIVERSAL CURRENCY

Metabolic rate is widely regarded as a universal currency in animal biology and ecology, providing an objective measure that can be used in attributing a cost to different activities and specifically helping to assess what animals do against some optimal behaviour (*i.e.* a behaviour that maximizes one or more biological characteristics such as growth or reproductive success). In their seminal paper, Brown *et al.* (2004) proposed that, 'Metabolism provides a basis for using first principles of physics, chemistry, and biology to link the biology of individual organisms to the ecology of populations,

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communities, and ecosystems'. From an ecological perspective, attributing a biologically meaningful cost to specific activities under different environmental circumstances helps to inform a wider understanding of the selective advantage of making trade-offs between different activities.

For fishes, understanding the balance of costs and benefits is complex. Most fishes are ectothermic, with body temperatures and therefore metabolic rates affected by their local thermal environment. Although movement in an aquatic environment is less costly when compared with terrestrial or aerial animals (Schmidt-Nielsen, 1972), understanding the balance of costs and benefits is further complicated by the patchy and relatively (assumedly) unpredictable distribution of resources, *e.g.* food and oxygen, in space and time, making it effectively impossible to predict, from basic principles, how a fish is likely to respond to a given external environmental situation or internal physiological state or need.

For many species of fishes, the choice between being active or inactive at different times of the day will affect both feeding success (Bestley *et al.*, 2008; Murphy *et al.*, 2011) and the risk of predation (Stuart-Smith *et al.*, 2007; Béguyer-Pon *et al.*, 2012). Measuring energy turnover, and the ways in which energy is allocated to specific activities, is therefore of central importance to understanding behavioural and physiological ecologies. For example, while aerobic metabolism is some 40 times more energy efficient than anaerobic metabolism, it has been shown that both wild (Neuenfeldt *et al.*, 2009) and captive (Claireaux *et al.*, 1995) Atlantic cod *Gadus morhua* L. 1758 will venture briefly into hypoxic waters to exploit a food resource, returning to well-aerated waters to digest the prey. From a physiological point of view, the decision to venture into hypoxic water to forage will depend on factors such as temperature (higher temperatures increase metabolic rate and so presumably militate against prolonged oxygen deprivation), the energy that must be expended in swimming to locate the prey and the probability that a foraging event will be successful. While there is scope to model such situations using, for example, dynamic energy budget (DEB) approaches (Teal *et al.*, 2012), there remains a need to compare model predictions with real outcomes in order to advance understanding of behavioural decision making, that is, how often do real animals get it wrong, by how much, and with what consequences?

To advance in such areas of behavioural and physiological ecology, there is a need to quantify the cost of the activities an animal undertakes. For instance, in the example mentioned above, how much energy does *G. morhua* expend when making a foraging trip into hypoxic water, both by swimming, and through having to respire anaerobically, and how much energy does it gain from the prey it captures, given that not all foraging events will be successful.

## MEASURING ENERGY METABOLISM

Ideally, energy metabolism should be estimated directly by measuring heat output (calorimetry) (Walsberg & Hoffman, 2005; Pakkasmaa *et al.*, 2006; Penttinen & Kukkonen, 2006). But, calorimetry has not previously been easily tractable with fishes given their relatively low mass-specific metabolic rates (Schmidt-Nielsen, 1997) and the high specific heat capacity of water (*c.* 4.2 *v.* 1.0 kJ kg<sup>-1</sup> K<sup>-1</sup> for air). Recently, however, a design for an inexpensive calorimeter that allows accurate measurement of

heat output from fishes to be measured in the laboratory has been described (Regan *et al.*, 2013). Nonetheless, metabolic rate in fishes has previously, and is usually still, estimated using indirect methods.

Because it is relatively easy to achieve in a laboratory situation, the most commonly used indirect method for quantifying metabolic rate in animals is to measure their rate of oxygen consumption ( $\dot{M}O_2$ ) (Clarke & Johnston, 1999). Indirect methods have both advantages and disadvantages, *e.g.* measuring oxygen consumption rate does not easily capture levels of anaerobic metabolism, nor is it good at capturing changes in metabolism over very short periods (s). Most methods for measuring  $\dot{M}O_2$  also require the fish to be in a steady state of rest or exercise and in some form of experimental chamber (respirometer), making the measurement of  $\dot{M}O_2$  in free-ranging animals impossible. There has, therefore, been considerable effort spent in trying to identify other indirect methods for quantifying energy metabolism that can be used in free-ranging animals, usually referred to as field metabolic rate (FMR).

Methods for quantifying FMR include the use of electromyogram (EMG) telemetry (Hinch & Rand, 1998; Cooke *et al.*, 2004), doubly labelled water (DLW) (Shaffer, 2011) or heart rate ( $f_H$ ) (Gilman & Wells, 1993). EMG telemetry involves measuring bioelectrical voltage changes in the muscle of the subject and has provided useful insights into the activity and behaviour of free-ranging animals, including fishes (Hinch & Rand, 1998). DLW measures the animal's carbon dioxide production by monitoring relative changes in stable isotopes of oxygen and hydrogen (Speakman, 1998). DLW can be used for air breathers, including mammals (Nagy, 2005), reptiles (Bennett & Nagy, 1977) and birds (Masman *et al.*, 1988; Shaffer *et al.*, 2001; Mullers *et al.*, 2009), but not for fishes because the high water flux across the gills and the low metabolic rate result in only small changes in divergence of the isotope concentrations (Speakman, 1997). In contrast, heart rate has been shown to provide a reasonably useful estimate of energy metabolism in large (>1 kg) teleosts (Clark *et al.*, 2005; Casselman *et al.*, 2012), although limitations include high equipment costs, poor reliability (Butler *et al.*, 2004) and variable relationships between heart rate and oxygen consumption rate (Thorarensen *et al.*, 2005; Iversen *et al.*, 2010). Fishes regulate cardiac output by changing heart rate, stroke volume or both, but where changes in cardiac output are largely a consequence of changes in stroke volume, heart rate may not be a good measure of oxygen consumption rate. Both the heart rate and DLW methods involve uncertainties and so, for fishes, these methods do not provide behavioural and physiological ecologists with comprehensive tools for the study of FMR and, until recently, there have been no robust methods for estimating metabolic rate in freely ranging fishes.

Recently, a new telemetric method for quantifying energy metabolism of free-ranging animals has been applied, that involves recording their movements, or more specifically their accelerations, in three dimensions (Wilson *et al.*, 2006). This method is equally applicable to all taxa of animals, as long as the individual is large enough to carry the device, and can easily be applied in both laboratory situations (for validation and calibration of the method) and the wild.

## MOVEMENT AND ACCELEROMETRY

Movement is one of the four main bodily functions which incur energetic costs in both endotherms and ectotherms (including fishes), the other three being: (1) basal

metabolic rate (BMR) (Frappell & Butler, 2004), (2) temperature effects on energy expenditure (Beamish & Trippel, 1990) and (3) specific dynamic action (SDA) (McCue, 2006). These latter three are perhaps most easily modelled since estimates are accessible *via* allometric relationships and they vary less in time, space and extent than do movement-associated energetic costs (Claireaux *et al.*, 2006; Fitzgibbon *et al.*, 2007; Jordan & Steffensen, 2007). Movement-induced energy expenditure is governed by muscle contractions and is typified by variable acceleration of the body (Gleiss *et al.*, 2010) so records of the tri-axial acceleration of fishes should provide a useful proxy for activity-specific energy expenditure. Indeed, based on this, recent studies have already correlated dynamic body acceleration (DBA, derived from tri-axial acceleration measurements) with oxygen consumption rate for a range of terrestrial and aquatic species, including cane toads *Bufo marinus* (Halsey & White, 2010), cormorants *Phalacrocorax carbo* (Wilson *et al.*, 2006), hammerhead sharks *Sphyrna lewini* (Griffith & Smith 1834) (Gleiss *et al.*, 2010) and European seabass *Dicentrarchus labrax* (L. 1758) (Wright *et al.*, 2014). Bi-axial acceleration (Clark *et al.*, 2010), the root-mean-square acceleration (Wilson *et al.*, 2013) and acoustically transmitted acceleration data (Murchie *et al.*, 2011) have also provided some exciting insights into fish behaviour and physiology.

## RECORDING ACCELERATION

Small electronic archival devices equipped with tri-axial accelerometers that are suitable for deployment on, or in, fishes are now commercially available from several manufacturers (Cefas Technology Ltd; [www.cefastechnology.co.uk](http://www.cefastechnology.co.uk): Star-Oddi; [www.star-oddi.com](http://www.star-oddi.com): Little Leonardo; [http://utbls.aori.u-tokyo.ac.jp/Bio-logging\\_Devices.html](http://utbls.aori.u-tokyo.ac.jp/Bio-logging_Devices.html)). There are also devices available that can transmit acceleration data that have been recorded and integrated over short periods of time. The archival device manufactured by Cefas Technology is typical, being 40 mm × 28 mm × 16.3 mm, weighing 18.3 g in air and 4.6 g in seawater. Devices are programmable and can record acceleration data at up to 30 Hz and can record other environmental data such as temperature and pressure. With a memory capacity of 56 MB, such devices can typically record and store acceleration data at 30 Hz continuously for up to 21 days. Through the use of delayed start (to allow recovery from surgery) and an appropriate data logging regime (*i.e.* recording periods interspersed with non-recording periods) that target recording at times of biological interest, however, both field and laboratory deployments can run for many months. During recording periods, the device records raw acceleration data in three planes of motion (Fig. 1), the X (dorso-ventral, heave), Y (side to side, sway) and Z (anterior-posterior, surge).

## CALCULATING ACCELERATION METRICS

Typically, once downloaded after a period of deployment, the raw X, Y and Z acceleration data are first processed to provide a time series of DBA. Overall DBA (ODBA) and vectorial DBA (VeDBA) can both be derived from the acceleration data. ODBA is calculated by summing the dynamic acceleration of the fishes, and has been shown to be a marginally better proxy for oxygen consumption rate for a range of species including

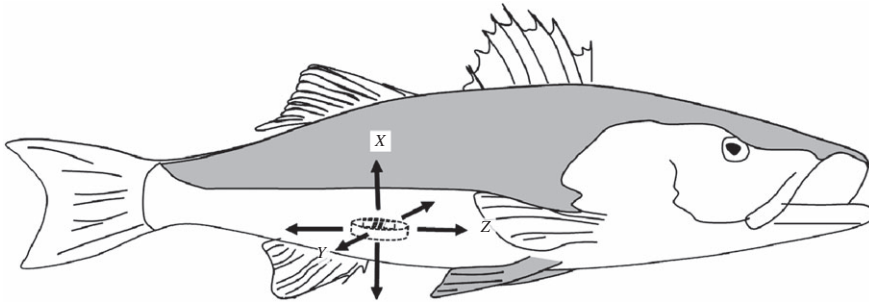


FIG. 1. Schematic diagram of a *Dicentrarchus labrax* implanted with a Cefas G6a data-storage tag. Arrows indicate the X (heave), Y (sway) and Z (surge) axes of acceleration recorded by the device (data from Wright *et al.*, 2014).

humans (Qasem *et al.*, 2012). In situations where the orientation of the device is not necessarily aligned precisely with respect to the vertical, VeDBA (vectorial sum of dynamic acceleration) may be a better proxy (Qasem *et al.*, 2012); for example, a direct comparison between ODBA with VeDBA for *D. labrax* with accelerometers implanted into the peritoneum indicates that VeDBA gives a marginally better fit with oxygen consumption rate (Wright *et al.*, 2014). ODBA and VeDBA are both calculated by firstly removing the static component of acceleration (the acceleration due to gravity) from the acceleration time series using the method described by Shepard *et al.* (2008). Briefly, this involves using a 2 s smoothing algorithm that has previously been shown to be appropriate for separating the static from the dynamic accelerations. Data are then converted to absolute values to reflect the change in acceleration from zero (irrespective of the values being negative or positive) before the vectorial sum (VeDBA;  $a$ ) or the sum (ODBA;  $b$ ) is calculated using the following equations:  $a = \sqrt{A_X^2 + A_Y^2 + A_Z^2}$  and  $b = A_X + A_Y + A_Z$ , where  $A_X$ ,  $A_Y$  and  $A_Z$  are the absolute dynamic acceleration values measured in the X, Y and Z axes, respectively (*cf.* Qasem *et al.*, 2012; Wright *et al.*, 2014).

## ACCELEROMETRY FOR ESTIMATING ENERGY EXPENDITURE

Several studies with fishes have now been published that show that DBA (either as ODBA or VeDBA) is well correlated with oxygen consumption rate offering a very valuable tool for estimating energy metabolism. These include *S. lewini* (Gleiss *et al.*, 2010) and *D. labrax* (Wright *et al.*, 2014), the latter across a range of temperatures (5–17°C) (Fig. 2).

Although accelerometry cannot provide measures of BMR, the effects of temperature on metabolic rate or SDA, a particular advantage of accelerometry is that, unlike oxygen consumption rate, it can capture energy expenditure associated with anaerobic metabolism [by measuring the excess post-exercise oxygen consumption (EPOC) associated with anaerobic activity] and movements that occur over very short periods of time. The acceleration data can also be analysed in detail to identify, and associate energetic cost with, specific movements and behaviours (Gleiss *et al.*, 2011, 2013; Broell *et al.*, 2013).

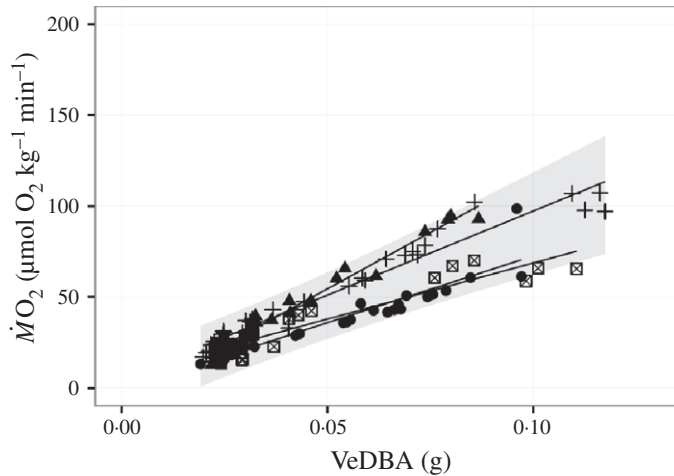


FIG. 2. Oxygen consumption ( $\dot{M}O_2$ ) in relation to vectorial dynamic body acceleration (VeDBA) for four individual (+, ●, ▲, ⊠) *Dicentrarchus labrax* at 6° C (data from Wright *et al.*, 2014). Fish were swimming in a flume at controlled swimming speeds, but at lower speeds and never forced to swim at, or close to, critical swimming speed ( $U_{crit}$ ); therefore, swimming was fully aerobic. Water oxygen tension was measured at 5 Hz, but oxygen consumption rate was calculated over a period of 10–25 min, DBA was recorded at 30 Hz.

## ACCELEROMETRY FOR ADVANCING THE UNDERSTANDING OF FISH SWIMMING CAPABILITIES

The swimming capabilities of fishes, and how these are affected by the physiological state of the fish and its environment, are a fundamental part of predicting how well fishes are likely to cope with environmental change (*e.g.* increased temperature or pH, or decreased oxygen availability) and for developing conservation interventions that may mitigate the effects of anthropogenic activities (*e.g.* fish passes around weirs or hydroelectric facilities). Swim tunnel studies have frequently been used to shed light on relationships between swimming speed (or performance) and metabolism in fishes (Claireaux & Lagarde're, 1999; Gleiss *et al.*, 2010; Steinhausen *et al.*, 2010) and, since its inception by Brett (1964), critical swimming speed ( $U_{crit}$ ), the speed at which it is generally assumed that maximum oxygen uptake occurs (Webb, 1975; Farrell & Steffensen, 1987; Keen & Farrell, 1994; Gregory & Wood, 1999), has become one of the most commonly used swimming performance tests for fishes.

Typically, measurements of  $U_{crit}$  are made using a swim tunnel or flume. The fish is placed into the swim tunnel and allowed to acclimate to the experimental situation and recover from handling stress at low speeds for a few hours. Water speeds generally are not higher than 0.5 body length per second ( $L_B s^{-1}$ ; Beamish, 1978) and the recommended recovery duration from handling is 8–12 h, although an increasing number of studies have shown no significant difference in  $U_{crit}$  between fishes left to recover overnight and fishes left to recover for 1–2 h (Peake *et al.*, 1997; Kolok, 1999; Farrell, 2007) and although other optimum recovery times may be different when trying to estimate other metrics of metabolic performance. After the recovery period, the water speed is increased at fixed speed and time increments and the fish swims, by rheotaxis, against the current. Fishes tend to hold their position against the current but, in some

early studies, electrified downstream screens were used to encourage the fish to swim against the current (Beamish, 1978). After several time intervals and speed increments, the fish fatigues and is swept to the screen at the end of the tunnel. This event defines the end of the test and  $U_{crit}$  can then be calculated as described by Brett (1964).

There is increasing evidence to show that forced swimming tests do not truly reflect the natural swimming capacities of fishes (Hammer, 1995; Plaut, 2001; Nelson *et al.*, 2002). Novel environments may cause the fish to behave abnormally for prolonged periods, resulting in an increased oxygen uptake (Wendelaar Bonga, 1997) and issues may arise due to the size or design of the swim tunnel (Tang & Boisclair, 1993), with animal movement potentially limited at crucial times such as during gait transition (Peake & Farrell, 2004). Flumes and swimming tunnels restrict the swimming behaviour to rectilinear swimming and flume design, specifically chamber length, affects gait expression by restricting behaviours based on moving forward and backward in a current. Thus, as fishes approach  $U_{crit}$ , they tend to shift from a steady swimming gait to the unsteady burst-and-coast gait, involving a rapid upstream burst followed by coasting back downstream.

Burst-and-coast swimming is an energy-saving behaviour increasing endurance at higher swimming speeds (Weihs, 1974). Therefore, the ability to exploit the burst-and-coast gait fully would be expected to affect maximum speeds attained before fatiguing. Haro *et al.* (2004) showed that fishes in a long (24 m) raceway reached higher swimming speeds than in a shorter flume, a result supported by studies of Castro-Santos (2004, 2005) and Peake & Farrell (2006). Tudorache *et al.* (2007a, b) showed that a swimming section shorter than 3.5 body lengths can significantly reduce critical swimming speed values in carp *Cyprinus carpio* L.1758 by impairing and reducing the duration of burst-and-coast swimming behaviour during a critical speed test. Additionally, Tudorache *et al.* (2010a, b) confirmed this finding by measuring blood and muscle lactate concentrations in brook charr *Salvelinus fontinalis* (Mitchill 1814) after swimming in short or in long swimming sections and being sampled before and after burst-and-coast swimming behaviour occurs. Gait transition speed, the speed at which the first burst-and-coast movement occurred, was not, however, affected by flume length, indicating that fishes in a long flume swim longer and reach higher critical swimming speeds when able to use burst-and-coast swimming. These results suggest that volitional swimming tests based on preferred swimming speeds and gait transition speeds using gradient flumes probably provide more realistic estimate of a fish's swimming capacities.

This principle of a gradient flume (Fig. 3) in which the water speed changes along its length was first designed and used by Colavecchia *et al.* (1998) to measure burst swim activity in *S. fontinalis*. The design is based on the fact that, at any point along its length, the water flow is the product of water speed and the cross-sectional area. Therefore, by gradually increasing the cross-sectional area of the flume from the upstream end to the downstream end, the water speed gradually decreases because the total flow at every point must remain the same.

In swimming tests, fishes are acclimated by holding them in the downstream end at a low water speed. Upon release, they enter the water channel and swim upstream against increasing water speeds. With the help of an implanted tag (Peake & Farrell, 2004) or cameras (Peake, 2008) mounted along a transparent bottom of the channel, the position and therefore the swimming speed of the fish can be recorded and swimming behaviour such as gait transition speed (Peake & Farrell, 2004) and kinematics such as tail beat

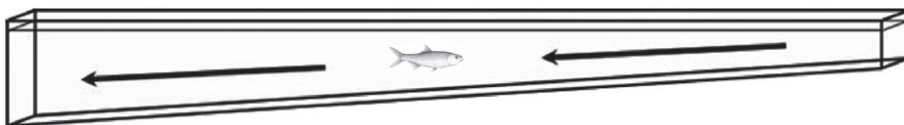


FIG. 3. A schematic three-dimensional drawing of gradient flume.  $\rightarrow$ , direction of the water flow (data from Tudorache *et al.*, 2013).

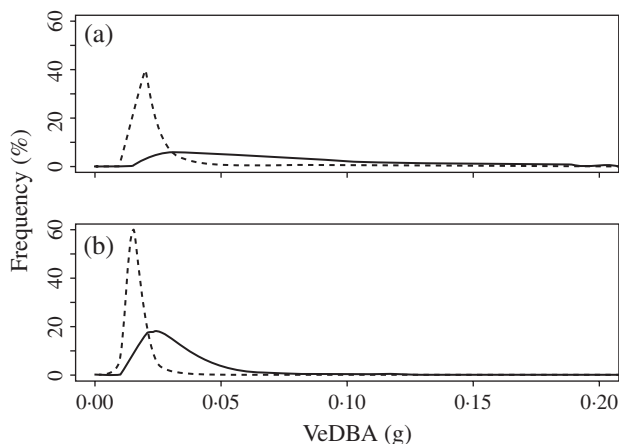


FIG. 4. Frequency distribution of vectorial dynamic body acceleration (VeDBA) for (a, b) two *Dicentrarchus labrax* across a range of swimming speeds whilst swimming in a flume (---) and swimming in a holding tank (—).

frequency and amplitude (Tudorache *et al.*, 2010*a, b*) can be analysed. The advantage of this system is that the fish swims totally volitionally, so swimming behaviour is more natural than when forced to swim at specific speeds in confined swimming sections of Blažka or Brett-type swimming tunnels. Also, the measurement of gait transition speed as an alternative to critical swimming speed, as suggested by Peake (2008), involves a less time-consuming protocol. A disadvantage of this design is that respirometry is not possible due to the large water volume necessary to achieve the range of water speeds. By comparing DBA at the same swimming speeds, however, it should be possible to assess differences in metabolic rate between forced and volitional swimming.

Combining methods that allow fishes to display their preferred and natural swimming behaviour with telemetry methods that can provide not only detailed information about movement (tail beat and gait) at fine temporal scales, but also information that can be used to estimate energy metabolism, offers great potential to improve the understanding of the swimming capabilities of fishes and how these are affected by physiological state and the environment. For example, distinct differences between restricted (*i.e.* in a flume) and free (in a holding tank) swimming behaviours can readily be resolved using acceleration data (Fig. 4), with fishes showing predominantly lower VeDBA values when swimming in the flume.

## LOGGERS V. TRANSMITTERS

Archival devices (loggers) provide continuously sampled acceleration at a high temporal resolution. Other recent studies have shown the value of using acceleration transmitters to track fishes (Wilson *et al.*, 2013). Bandwidth limitations, however, mean that acoustic devices are not able to transmit raw data at the high rates (10s of Hz) achieved by loggers and so acceleration transmitters integrate acceleration data over a period of a few seconds and then transmit, using acoustic transmission, integrated acceleration data. There are both advantages and disadvantages when using transmitted and logged acceleration. Both provide an overall activity level (DBA) metric, which can be used to calculate activity-specific energy use (Gleiss *et al.*, 2010; Wilson *et al.*, 2013). Logged acceleration can also be used to extract more detailed information about the behaviour of the animal (Whitney *et al.*, 2007, 2010; Broell *et al.*, 2013; Brownscombe *et al.*, 2013; Gleiss *et al.*, 2013) as a means to identify specific behavioural events including feeding (Broell *et al.*, 2013; Gleiss *et al.*, 2013), but it is not possible to extract these very short-term behaviours from the integrated information acquired using transmitters. On the other hand, unlike transmitters, loggers must be retrieved at the end of the study in order that the data can be downloaded. Researchers therefore need to select the appropriate recording or transmitting device depending on their research aims and the likelihood that devices can be easily retrieved at the end of the study.

## CONCLUSIONS

The correlations between DBA and oxygen consumption rate demonstrate that DBA can be used as a metric for estimating activity-specific metabolic rate in a range of fish species (Wilson *et al.*, 2006, 2013; Gleiss *et al.*, 2010; Wright *et al.*, 2014). Electronic data loggers (data storage tags) have previously been shown to provide unparalleled insights into the vertical movement and habitat selection of aquatic animals in the wild (Sims *et al.*, 2005; Metcalfe *et al.*, 2008; Righton *et al.*, 2010). Now, with the incorporation of tri-axial accelerometers, these devices promise to provide a robust method for estimating activity-specific metabolic rate in the field (Halsey *et al.*, 2011).

Acceleration data loggers can be implanted internally into fishes and, with an appropriate duty cycle, can have a long operating life. This permits DBA to be a useful proxy for estimating activity-specific energy expenditure from fishes in mesocosm or field studies over extended periods where other methods (*e.g.* conventional respirometry or calorimetry) would not be feasible. Details of the physiological inter-relationships between temperature, SDA, basal, standard and active metabolic rates would still need to be derived from laboratory studies before DBA could be used to provide complete, absolute estimates for FMR.

A specific advantage of accelerometers in relation to activity-specific energy expenditure is the capability to record very short periods of intense activity which, in most fishes, is achieved using white muscle. White muscle makes up the bulk of the muscle in most fishes (Greer-Walker & Pull, 1975) and white muscle activity is largely supported by anaerobic metabolism (Bond, 1979) functioning as an 'emergency power pack' during burst swimming. Short periods of intense activity powered by white muscle are often essential for predator avoidance or prey capture; behaviours that, particularly in the case of predator avoidance, can be critical to survival. Laboratory-based studies have been conducted that investigate anaerobic capabilities such as escape response

(fast-start) and sprint swimming in fishes (Ghalambor *et al.*, 2004; Marras *et al.*, 2010, 2011; Killen *et al.*, 2014). The methods used to measure energy expenditure in such studies, however, are not usually suitable to long-term mesocosm or field studies, making it difficult to investigate how the capacity to engage in short periods of intense activity in the wild, or in semi-wild situations, is affected by temperature or other environmental stressors (*e.g.* hypoxia, acidification and starvation).

Accelerometry offers the potential to overcome some of these limitations, making it possible to investigate the effects of a number of environmental stressors (alone and in combination) on both the aerobic and anaerobic capacities of fishes. Furthermore, this technology can be applied equally to both laboratory, important for ground-truthing, and field situations. Accelerometry therefore provides a tool to help, *inter alia*, understand how environmental stressors affect fish energetics in their natural environment and therefore shed light on how they make trade-offs between different activities that allows them to cope with environmental stress.

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