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Remote bioenergetics measurements in wild fish: Opportunities and challenges☆

Steven J. Cooke^{a,*}, Jacob W. Brownscombe^a, Graham D. Raby^b, Franziska Broell^c, Scott G. Hinch^d, Timothy D. Clark^e, Jayson M. Semmens^f^a Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Dr., Ottawa, ON, K1S 5B6, Canada^b Great Lakes Institute of Environmental Research, University of Windsor, 401 Sunset Ave., Windsor, ON, N9B 3P4, Canada^c Department of Oceanography, Dalhousie University, 1355 Oxford St., Halifax, NS, B3H 4R2, Canada^d Department of Forest & Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, BC, V6T 1Z4, Canada^e University of Tasmania and CSIRO Agriculture Flagship, 3-4 Castray Esplanade, Hobart, TAS 7000, Australia^f Fisheries and Aquaculture Centre, Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7001, Australia

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ABSTRACT

The generalized energy budget for fish (i.e., Energy Consumed = Metabolism + Waste + Growth) is as relevant today as when it was first proposed decades ago and serves as a foundational concept in fish biology. Yet, generating accurate measurements of components of the bioenergetics equation in wild fish is a major challenge. How often does a fish eat and what does it consume? How much energy is expended on locomotion? How do human-induced stressors influence energy acquisition and expenditure? Generating answers to these questions is important to fisheries management and to our understanding of adaptation and evolutionary processes. The advent of electronic tags (transmitters and data loggers) has provided biologists with improved opportunities to understand bioenergetics in wild fish. Here, we review the growing diversity of electronic tags with a focus on sensor-equipped devices that are commercially available (e.g., heart rate/electrocardiogram, electromyogram, acceleration, image capture). Next, we discuss each component of the bioenergetics model, recognizing that most research to date has focused on quantifying the activity component of metabolism, and identify ways in which the other, less studied components (e.g., consumption, specific dynamic action component of metabolism, somatic growth, reproductive investment, waste) could be estimated remotely. We conclude with a critical but forward-looking appraisal of the opportunities and challenges in using existing and emerging electronic sensor-tags for the study of fish energetics in the wild. Electronic tagging has become a central and widespread tool in fish ecology and fisheries management; the growing and increasingly affordable toolbox of sensor tags will ensure this trend continues, which will lead to major advances in our understanding of fish biology over the coming decades.

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1. Introduction

Marine and freshwater fish provide critical ecosystem services and play important roles in culture, society, the economy and spirituality (Holmlund and Hammer, 1999; Lynch et al. in press). As a consequence, fish are some of the most intensively managed and studied wild organisms. At the level of the individual fish, food consumption provides the fuel for cellular processes (Hochachka and Somero, 1980) and basic organism functions, including respiration, digestion, locomotion, growth, and reproduction (Tytler and Calow, 1985). Indeed, energy is the currency of life (Kleiber, 1975). The energetic status of an individual fish determines its reproductive output, which in turn,

impacts population-level processes (Tytler and Calow, 1985). Further, energy transfer via foraging (e.g., predation, scavenging) and excretion influence community and whole-ecosystem level processes. Not surprisingly, fish biologists and managers devote significant effort to refining our understanding of fish bioenergetics (Hansen et al., 1993) and apply related principles (e.g., energy transfer and productivity; Kitchell et al., 1974; Lapointe et al., 2013) to fisheries management.

The fundamental principles of fish bioenergetics are based on simple and ubiquitous mass-balance equations and thermodynamics, given that processes in fish are governed by water temperature (Brett and Groves, 1979; Tytler and Calow, 1985; Adams and Breck, 1990; Jobling, 1995). The generalized bioenergetics equation for fish (i.e., Energy Consumed = Metabolism + Waste + Growth) is as relevant today as when first reviewed by Brett and Groves in 1979. After early derivation of bioenergetics models for fish (e.g., Kitchell

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* Corresponding author.

E-mail address: steven.cooke@carleton.ca (S.J. Cooke).

et al., 1977; Rice and Cochran, 1984), a team at the University of Wisconsin developed computer software (i.e., the Wisconsin Bioenergetics Model [Hewett and Johnson, 1987]) with which users could easily manipulate model parameters to solve for growth or consumption and adapt existing models to other species (Ney, 1993). The Wisconsin Bioenergetics Model remains a popular tool in fisheries science and management (Hansen et al., 1993) although in recent years dynamic energy budgets have grown in popularity and represent the frontier in bioenergetics modeling, enabling testable estimates of the influence of environmental and ecological factors on aspects of fish bioenergetics such as growth and reproduction (Nisbet et al., 2000; Kooijman, 2010).

Bioenergetics modeling requires the input of reliable measurements of the components of the energy budget. Obtaining such measurements in wild fish is inherently challenging (Soofiani and Hawkins, 1985). For example, how does one determine how much a fish consumes on a daily basis? Or how much energy is expended on locomotion? Or the costs of digestion? Traditional approaches to estimating bioenergetics were based on data from fish in the laboratory (see Brafield, 1985), which were used to make extrapolations or inferences about fish in the field (see Ney, 1993). However, this is an obvious oversimplification of energy dynamics given the major effects that captivity can have on the behaviour and physiology of wild animals (Hansen et al., 1993). Parameterizing models for wild fish using ecologically relevant data that combine natural elements of behaviour, physiology, and ecology is changing the way we view fish energetics and providing managers and conservation practitioners with better tools for addressing real-world problems. This is accomplished mainly using electronic tagging technology—such as biologging and biotelemetry techniques that incorporate various types of sensors (Lucas et al., 1993; Cooke et al., 2004a; Wilmers et al., 2015). For decades, researchers have been using electronic tags to estimate components of the bioenergetics model (reviewed in Lucas et al., 1993; Cooke et al., 2004b); predominantly the activity component of metabolism. These tools have undergone continuous refinement, resulting in a number of commercially-available tags that have the potential to be used to estimate several components of the bioenergetics equation.

Quantifying animal bioenergetics in the wild has extensive potential for application in movement and behavioural ecology. For example, movement paths can be explained by the variable energetic costs of moving through different terrain or water currents (Wall et al., 2006; McElroy et al., 2012). Energy use can also explain modes of locomotion (Wilson et al., 1991), including gait transitions in fish (Peake and Farrell, 2004). Ecological energetics provide important mechanistic insight into how and why animals behave in the wild (Shepard et al., 2013; Tomlinson et al., 2014), yet this framework is rarely applied to fish due to constraints in simultaneously measuring fish position and quantifying energetics. However, recent advancements in biotelemetry and laboratory techniques provide methods that can be used to obtain such measurements (e.g., Burnett et al., 2014; Brownscombe, 2016). With these insights, we can make more informed predictions about the underlying mechanisms that create spatial and temporal patterns in fish distributions.

The objective of this paper is to review the state of electronic tagging tools as they relate to the study of bioenergetics of wild fish in the field. We acknowledge existing fish-centric syntheses that have focused on a specific technology (e.g., heart rate and opercular telemetry; Lucas et al., 1991; EMG telemetry, Cooke et al., 2004b; accelerometry, Metcalfe et al., 2015) which have largely focused on the activity component of the energetics model. There have also been several broad cross-taxa syntheses that reviewed the use of electronic tagging as a tool in ecology (Cooke et al., 2004a; Payne et al., 2014; Wilson et al., 2015). Here, we briefly review the suite of electronic tagging tools available (biotelemetry and biologging) that can be used in the study of bioenergetics. Next, we consider the generalized fish bioenergetics model and the ways in which the existing toolbox could be used to address each of its components. We conclude by identifying technical developments that need to occur

to properly address outstanding research gaps that impede our ability to comprehensively apply bioenergetics models to the study and management of wild fish.

2. A primer on the tools

Biotelemetry and biologging technologies can both be used to remotely collect behavioural and physiological information on wild fish and their surrounding environment. For biotelemetry, a signal emanating from a device carried by the animal (transmitter) sends data to a receiver. The power for transmission can be derived from an external energy source (e.g., as is used by Passive Integrated Transponders—or PIT tags) or internal energy source (i.e., battery). In biologging, data are recorded and stored in an animal-borne device (archival logger) and can be downloaded when and if the logger is retrieved. Additionally, there are an increasing number of techniques that couple the two technologies, first logging information onboard and then transmitting the information (often to a satellite) when possible. We acknowledge that other remote sensing techniques such as hydroacoustics (reviewed by Misund, 1997) and underwater videography (reviewed by Struthers et al., 2015) can also generate data that are relevant to fish energetics, yet these techniques are beyond the scope of this paper. We do cover image capture in the context of animal-borne devices.

Some of the earliest attempts to measure the energetics of fish in the field using electronic tagging tools extend back to the 1950s. However, it was only in the 1990s that “off-the-shelf” commercial tags became available. Early versions of devices were often a result of collaboration between ecologists and engineers, involving substantial research and development; this often remains the case today. Although we attempt to cover all relevant technologies in this paper, we focus on those that are currently commercially available and can therefore be readily adopted by researchers and managers. We note that the landscape of available electronic tags (especially sensors) is always changing and that papers (such as this) based on technology can rapidly become (at least partially) outdated so readers are encouraged to continue to consult the emerging literature and the websites of biotelemetry and biologger manufacturers.

2.1. Calibrating sensor tags to measure energy expenditure in fish

Heat output (calorimetry) is the most direct way to measure energy expenditure (Levine, 2005; Regan et al., 2013). However, this method is difficult to use with fish due to the high specific heat capacity of water (relative to that of air) combined with the often low mass-specific metabolic rates of fish (Walsberg and Hoffman, 2005). The most common method to quantify energy expenditure in fish is indirectly, using oxygen consumption (Metcalfe et al., 2015), which is also a common approach in other taxa (Halsey et al., 2009; Gleiss et al., 2011). This method involves measuring changes in oxygen concentrations in the water surrounding the fish, and is therefore restricted to fully- or partially-enclosed systems (i.e., intermittently-sealed or flow-through respirometers), and cannot be measured *in situ* with free ranging fish (Steffensen, 1989; Clark et al., 2013b). In the case of animal-borne sensor-tags (e.g., electromyogram [EMG], acceleration, or heart rate), most studies calibrate tag output with oxygen consumption rate and swimming speed using a swim tunnel respirometer (e.g., Booth et al., 1997; Clark et al., 2010; Gleiss et al., 2010; Wilson et al., 2013). Estimates of oxygen consumption rate can then be converted into units of energy (e.g., Joules or calories) using standard conversion coefficients specific to taxa and trophic position (Elliott and Davison, 1975), which enables integration into bioenergetics models. Nearly all fish are fully ectothermic, which results in their metabolic rate being highly dependent on water temperature (Fry and Hart, 1948; Brett, 1964; Clarke and Johnston, 1999). Temperature also plays an influential role in regulating the metabolism of endothermic/heterothermic fishes (Blank et al., 2007; Clark et al., 2013a). Therefore, to estimate energy

expenditure in the wild, it is important to calibrate the relationships between electronic tag output and energy expenditure across the ecologically-relevant range of temperatures for the study species (e.g., [Wilson et al., 2013](#); [Brownscombe et al., 2016](#)).

While calibration of sensor tag output with energy expenditure using a swim-tunnel respirometer is currently the best approach for understanding activity-related metabolism, it has its limitations. Swim tunnels are constricted environments that may cause artificial increases in oxygen consumption and restrict the swimming capacities of fish, especially during gait transitions ([Metcalf et al., 2015](#)) and in the vertical axis. Swim tunnels also generate laminar flow, which may not reflect actual conditions, including water turbulence, in the wild ([Roche et al., 2014](#)). Further, this approach only examines linear swimming, even though the energetic costs of turning can be significant. Using free-swimming, small-bodied brook trout (*Salvelinus fontinalis*), [Tang and Boisclair \(1995\)](#) showed that turning had a significant effect on energy expenditure in a respirometer. We are unaware of any research papers that have integrated behaviours more complex than steady-swimming into estimates of energy expenditure using electronic sensor tags. If the goal is to quantify the metabolic costs of digestion, then calibration of heart rate tags in static respirometers is most appropriate.

2.2. Acceleration sensors

Acceleration sensors measure acceleration (g-force, $1\text{ g} = 9.81\text{ m s}^{-2}$) at extremely high rates, up to thousands of samples per second in one to three axes. These sensors initially became available in the form of acceleration biologgers, which store the information in on-board memory (reviewed by [Brown et al., 2014](#)). For decades, this technology has been used to examine bioenergetics and diverse aspects of ecology, physics, animal behaviour, and physiology ([Nathan et al., 2012](#); [Payne et al., 2014](#)). When attached to an animal, acceleration biologgers record and store raw acceleration in up to three axes, which includes dynamic (animal movement) and static (gravity) acceleration. In the analysis phase, these two components can be distinguished to provide fine-scale information on locomotion and body posture (see [Shepard et al., 2008](#)). These data are useful for remotely quantifying animal behaviour and activity-related energy expenditure ([Brown et al., 2014](#)). While acceleration biologgers provide very detailed information, a limitation in the study of wild fish is the need to recapture the loggers so that data can be retrieved ([Metcalf et al., 2015](#)). More recently (since 2008), acceleration sensors have been integrated into acoustic transmitters, which do not transmit raw acceleration data, but a summarized acceleration value that provides an index of activity. This approach cannot be used to quantify behaviour in the detail that is possible using raw acceleration data and instead, provides a coarse measure of 'animal activity' or an estimate of the number of times a pre-defined behavioural event occurred (see details below). The advantages of acceleration transmitters are that a) they can be used to provide data for weeks or months, whereas acceleration loggers are often restricted to <10 days of data, and b) tag recapture is not required for data acquisition (e.g., [Stehfest et al., 2015](#); [Gannon et al., 2014](#); [Murchie et al., 2011](#)). Use of algorithms to classify behaviours onboard devices and thus reduce the need for large storage quantities will presumably enable longer-term field deployments of acceleration loggers (e.g., see [Naito et al., 2013](#)).

2.2.1. Acceleration biologgers

Acceleration biologgers have been used to make empirical measurements of behaviour and energy expenditure but primarily in terrestrial and semi-aquatic animals ([Brown et al., 2014](#)). More recently, researchers have begun applying this technology to fish (e.g. [Whitney et al., 2007](#); [Clark et al., 2010](#); [Gleiss et al., 2010](#); [Watanabe et al., 2012](#); [Broell et al., 2013](#); [Brownscombe et al., 2014](#); [Wright et al., 2014](#)). Some of the earliest studies used two-axis acceleration-sensor data loggers to assess activity levels in Japanese flounder (*Paralichthys olivaceus*; [Kawabe et al., 2004](#)) and chum salmon (*Oncorhynchus keta*;

[Tanaka et al., 2001](#)) although three-axis sensors are now more common. To date, most studies on fish have focused on general patterns in behaviour and activity, with few estimating energy expenditure (but see [Gleiss et al., 2010](#); [Wright et al., 2014](#)). To our knowledge, acceleration biologgers have yet to be used to estimate energy expenditure in fish in the wild.

Calibration of acceleration biologger output with energy expenditure is typically accomplished using the swim tunnel method (see Section 2.1 above). Most applications use tri-axial accelerometers, which measure acceleration in surge (forward, y), heave (vertical, x), and sway (horizontal, z) axes. The absolute sum of dynamic acceleration in each axis (i.e., when acceleration due to gravity is removed) is commonly referred to as overall dynamic body acceleration (ODBA), which is termed partial dynamic body acceleration (PDBA) when based on one or two acceleration axes ([Gleiss et al., 2011](#); [Metcalf et al., 2015](#)). Experimental calibrations have found relationships between these metrics (particularly ODBA) and metabolic rate in a range of taxa, with marked differences among species ([Halsey et al., 2009](#); [Gleiss et al., 2010, 2011](#); [Wright et al., 2014](#)). More recently, [Qasem et al. \(2012\)](#) and [Wright et al. \(2014\)](#) suggest vectorial dynamic body acceleration (VeDBA) may be a better correlate with oxygen consumption rate in animals, including fish, especially when logger orientation is inconsistent. Interestingly, a recent study on flatfish found better relationships between tailbeats (measured from acceleration) and metabolic rate than when ODBA or VeDBA were calculated and regressed against metabolic rate (see [Mori et al., 2015](#)).

Battery life is limiting to deployment duration and sampling frequency when using acceleration biologgers, which typically last days or weeks in wildlife applications. The minimum necessary recording frequency is related to the stroke frequency of the animal ([Shepard et al., 2008](#)). In general, greater frequencies increase the accuracy of energy expenditure estimates and increase the likelihood of identifying fine-scale behaviours ([Gleiss et al., 2011](#); [Broell et al., 2013](#)), but also decrease battery life and therefore deployment duration. Despite the fact that many acceleration biologgers can measure at high sampling frequencies (e.g., hundreds of samples per second; 300 Hz), studies have shown that relatively low sampling frequencies (e.g., 10 Hz) can be used to make reasonably precise estimates of the energy expenditure required for locomotion ([Wilson et al., 2008](#)). Loggers can also be set to record in duty cycles (e.g., 1 h per day, or only once a critical acceleration threshold is reached) to increase deployment duration. Some vendors offer delayed starts so that animals can recover from tagging stress before the device begins to log data.

The fact that acceleration biologgers must be recaptured is the main logistical challenge in their use, a problem that is particularly pronounced in fishes. However, some fishes have high site fidelity (e.g., bonefish, *Albula* spp.), or make predictable movements or migrations (e.g., salmonids), traits that make field experiments with acceleration biologging more feasible. Recent advancements have enabled tightly-secured attachment of tags (which is required for acceleration biologging) paired with timed releases ([Watanabe et al., 2008](#); [Whitmore et al., 2016](#)). However, electronic tags that combine multiple sensors, transmitters, and release mechanisms (i.e., to facilitate recapture or transmission of information to receivers) are currently limited to large-bodied animals; animals for which laboratory-based calibration experiments (e.g., involving swim-tunnel confinement) are sometimes impossible (although see [Payne et al. \(2015\)](#) for an approach to swimming large species).

2.2.2. Acceleration transmitters

There are two types of accelerometer transmitters reported in the literature. The most common is a tag manufactured by VEMCO (Bedford, NS, Canada; hereafter referred to as activity tags). Activity tags measure acceleration at a rate of either 5 or 10 Hz (depending on programming and tag type) in two (lateral (z) and vertical (x)) or three (forward (y), lateral (z) and vertical (x)) axes at a set sampling interval

(e.g., 30 s of measurements every 90 s). Static acceleration (that due to gravity) is filtered out of the data using pass filter that passes data above 4 s or 25 Hz, resulting in the acceleration from the motion of the tagged animal (dynamic acceleration). The root mean square (RMS) or resultant vector of the x, z or x, z, y dynamic acceleration is calculated (e.g., $\sqrt{x^2 + z^2}$ or $\sqrt{x^2 + z^2 + y^2}$), averaged over the sampling period and then stored in memory. This RMS value is then transmitted during the next transmission cycle. Although coarser because the data are averaged and binned, the RMS values from activity tags are analogous to *PDBA* and *VeDBA*, which can be calculated at a fine temporal scale from accelerometer logger data, as described above. The second type of accelerometer transmitter represents a new development that attempts to overcome limitations on the behavioural insights typically provided by transmitters via on-board identification of behavioural classes (e.g., as suggested in [Broell et al., 2013](#)). This method has been recently implemented using 'AccelTag' ([de Almeida et al., 2013](#)) (See *Quantifying foraging in the wild* below).

The RMS values from activity tags have been calibrated with oxygen consumption rates using the swim tunnel approach (see Section 2.1 above), and the resultant relationships used to estimate field metabolic rates associated with locomotion in cuttlefish *Sepia officinalis* ([Payne et al., 2011](#)) and bonefish *Albula vulpes* ([Murchie et al., 2011](#); [Brownscombe et al., 2016](#)). In sockeye salmon, activity tag output was calibrated with swimming speed and oxygen consumption rate across a range of temperatures ([Wilson et al., 2013](#)); the swimming speed calibrations were then used to estimate swimming speeds in fish migrating through areas with high tidal currents in the marine environment ([Wilson et al., 2014](#)) and in salmon attempting to ascend a vertical slot fishway in freshwater ([Burnett et al., 2014](#)). Some studies have used activity tags to investigate the fundamental relationship between temperature and bioenergetics in ectotherms. [Neuheimer et al. \(2011\)](#) calibrated activity tag output with swimming speeds in the reef fish *Cheilodactylus spectabilis* across a range of temperatures, subsequently deployed the tags in the field to estimate swimming speeds during spawning, and assessed how increases in water temperatures, observed in their geographic range, may impact their ability to reach the required swimming speeds for spawning. [Gannon et al. \(2014\)](#) used activity tags to demonstrate that seasonal accelerometer values from a wild predatory fish *Platycephalus fuscus* approximated a typically-shaped temperature performance curve, with values peaking at an apparent optimal temperature (T_{opt}) and then declining with increasing temperatures. The performance curve for tag activity output appeared to match with catch-per-unit effort data for the same species ([Gannon et al., 2014](#)). In the related *P. bassensis*, there was an ~8% increase in activity tag values for each 1 °C increase in temperature, although this relationship continued throughout the range of temperatures at which measurements were made, preventing prescription of a T_{opt} ([Stehfest et al., 2015](#)). We caution that higher activity levels are not necessarily advantageous from a bioenergetics perspective, and thus should not (on their own) be used to identify ecologically optimal temperatures. Indeed, higher activity levels can result in significantly reduced growth and fitness ([Boisclair and Leggett, 1989](#); [Rennie et al., 2005](#)).

Activity tags have also been used to examine foraging behaviour in predatory fish, including in *Sphyrna barracuda* ([O'Toole et al., 2010](#)) and *Acanthopagrus australis* ([Taylor et al., 2013](#)), with time spent foraging a key component of bioenergetics models. [Payne et al. \(2013\)](#) used activity tags to show that the estuarine-associated *A. australis* switched from a diurnal to a nocturnal activity pattern following rain and then back to predominantly diurnal activity once environmental conditions had stabilised. Similarly, [Wilson et al. \(2014\)](#) used activity tag data calibrated with swim speed to show that *O. nerka* migrating to spawning grounds swam at metabolically optimal speeds in the marine environment, but at supra-optimal speeds once migrating upstream through a river. There was also a diel difference in the activity tag data, with fish apparently swimming at higher speeds during the

daytime. Documenting changes in activity is important for developing energy budgets that are tailored to location, environmental conditions, or temporal variables (e.g., seasonality or diel patterns).

2.3. Electromyogram sensors

Electromyograms (EMGs) are bioelectrical voltage changes that are roughly proportional to the degree and duration of muscle tension ([Sullivan et al., 1963](#)). In the laboratory, EMGs can be measured using hard-wired systems where paired electrodes are placed in muscle tissue (often axial swimming muscle but can also be placed in mandibular or opercular tissues) and connected to monitoring systems that amplify and record the signal.

The first study to adopt EMG technology for remote measures detected EMGs from the adductor mandibulae (muscle responsible for closing the mouth) of brown trout and transmitted the output using acoustic telemetry ([Oswald, 1978](#)). By analysing the transmitted EMG signals, feeding was distinguished from other types of activities, such as coughing. Tagged fish were released in a lake, and feeding activity and ventilatory rhythms were monitored in free-living fish for extended periods ([Oswald, 1978](#)). A similar acoustic transmitter was implanted in the lateral musculature and used for continuous monitoring of tail-beat frequency in free-swimming trout ([Ross et al., 1981](#)) with other efforts focused on developing similar technology in radio transmitters ([Sayre, 1978](#); [Luke et al., 1979](#); [Weatherley et al., 1980](#); [Patch et al., 1981](#); [Rogers et al., 1981](#)). These studies represented some of the first in which researchers were able to calibrate electronic tags in the laboratory and then remotely measure EMGs from fish to estimate energetic parameters ([Weatherley et al., 1982](#)). The same radio device was used to relate EMG signals recorded from levator arcus palatini, a small muscle involved in the opening of the gill operculum, to oxygen consumption in rainbow trout ([Rogers and Weatherley, 1983](#)).

Researchers involved with some of the early work on EMG radio telemetry collaborated closely with electronic engineers from Lotek Engineering Inc. (now Lotek Wireless Inc.) and developed the only remote EMG device that has become commercially available (see [Kaseloo et al., 1992](#); [Hinch et al., 1996](#)). The device that was commercialized consisted of an epoxy coated transmitter package, two paired, Teflon-coated stainless steel electrode wires, and a whip antenna. The two electrodes of the surgically implanted EMG transmitter were implanted in musculature which was somewhat limiting. The EMGs were transmitted as radio pulses, with the intensity of muscular activity determining the intervals between pulses which was recorded by the radio receiver ([Kaseloo et al., 1992](#)). This design of EMG transmitter does generate some problems as the values derived represent a "black box" (see discussion in [Cooke et al., 2004b](#)). More recently, the commercial manufacturer has produced a coded EMG transmitter (Lotek Engineering Inc., CEMG-R11-25). The voltage corresponding with muscle activity is rectified and then sampled over a 3-second time period. These individual samples are summed and stored until the end of the 3-second period when the average value is determined and assigned an activity level that ranges from 0 to 50. These activity levels are transmitted to the telemetry receiver. In addition to the different methods in signal transmission, the coded nature of the transmitters now permits multiple transmitters to be monitored simultaneously on the same frequency. A common problem with both tag types is that they are sensitive to the positioning of the electrodes as well as significant inter-tag variation in performance ([Beddow and McKinley, 1999](#); [Brown et al., 2007](#)). As a consequence, to achieve rigorous calibrations between EMG output, swimming speed, and energy expenditure, calibration experiments must be done on the same individuals to be released into the field for remote measurements ([Miyoshi et al., 2014](#)).

EMG radio tags were widely used during the mid-1990s through mid-2000s with studies of fish in freshwater. The use of EMG tags has become less common in recent years (but see [Makiguchi et al., 2011](#); [Miyoshi et al., 2014](#); [Taylor et al., 2014](#)) given that the coded tags no

longer provide the ability to document burst swimming activity reliably. Moreover, relative to say accelerometer devices, surgical implantation and detailed placement of electrodes is required. Beyond the radio tag platform, the output module has been modified to transmit acoustic waveforms (Dewar et al., 1999; Lembo et al., 2008) although we are unaware of any studies that have applied that technology in the field. Similarly, we are unaware of any researchers that have developed biologgers that measure EMGs for use in wild fish.

2.4. Heart rate sensors

Heart rate (f_H) is modulated in most animals to adjust blood flow and oxygen transport, and therefore it can act as a proxy for metabolism and energy expenditure (Butler et al., 2004; Green, 2011). While some studies suggested that fishes differed from most other vertebrates by modulating cardiac output more so via changes to stroke volume rather than via f_H (Thorarensen et al., 1996), insufficient recovery periods following anaesthesia and instrumentation may have masked the true prevalence of f_H modulation in fishes (Clark et al., 2005). Notably, because f_H is a 'central' measurement in the circulatory system, it is typically implicated in all aspects of bioenergetics relating to tissue oxygen demand rather than just reflecting the energetic cost of locomotion (cf. Green et al., 2009; Gleiss et al., 2010, 2011; Green, 2011), and thus can provide information on parameters such as meal size and specific dynamic action in addition to activity-related metabolism (Priede, 1983; Lucas and Armstrong, 1991).

Heart rate sensors usually detect electrocardiograms (ECG) but can also be based on other measurements such as electrical impedance or the physical movement of the heart (Clark et al., 2008). Techniques often involve placement of electrodes (attached by wire to the device) near the pericardial cavity within the coelom (Clark et al., 2008) or in muscles ventral to the heart (e.g., Claireaux et al., 1995; Cooke et al., 2001). Some devices have the electrodes on the surface of the tag, which can then be placed in the stomach (i.e., gastric implant; Lucas, 1992; Armstrong et al., 1989) or adjacent to the pericardial cavity (e.g. Star Oddi heart rate loggers). A common problem with ECG devices is proper placement of electrodes and maintaining electrode position throughout long deployments (Cooke et al., 2004b).

ECG sampling frequencies of around 100 Hz are typically satisfactory for assessments of f_H in fishes, but higher sampling frequencies may enhance the signal-to-noise ratio by capturing the absolute peak of the R-spike in the ECG waveform. Some devices detect and record the entire ECG waveform, while others detect and process the waveform but only provide a mean f_H over defined durations (e.g., mean f_H in 10 s). The latter approach dramatically saves on-board data storage space and/or reduces the amount of data to be transmitted. On-board processing however, precludes an investigation of other aspects of the ECG waveform that may be useful for understanding attributes such as fish health (e.g., via f_H variability; Altimiras et al., 1995, 1996), and assumes that the f_H values being generated are robust to changes in tag position or electrical noise. In any event, few studies have calibrated f_H against energy expenditure (~oxygen consumption rate) using electronic tags in order to estimate the latter from the former. In this context, the scientific question and study species/system will dictate the decision on how f_H sensors are configured and whether logging or transmitting devices are used. The general pros and cons for f_H loggers versus transmitters are similar to those outlined above for acceleration and EMG devices, and thus will not be repeated here.

Heart rate has been measured remotely in fish for over 5 decades (e.g., Lonsdale, 1969; Wardle and Kanwisher, 1973; Priede and Tytler, 1977) but there are still relatively few devices that have been produced commercially (e.g., heart rate loggers by Star Oddi and those in Clark et al. (2005, 2010); f_H acoustic telemetry devices by Thelma BioTel and Vemco). There has been infrequent but steady use of such devices since their inception but they have never become commonplace within the research community which is attributable to a combination of the

perceived lack of market (for commercialization) and the technical challenges with the use of such devices. Researchers that have worked with such technology often describe it as being fraught with technical challenges.

2.4.1. Heart rate biologgers

The majority of f_H measurements made in free-swimming, untethered fishes have been recorded using animal-borne data loggers. Still, papers reporting on the use of f_H loggers in fish have only been published sporadically, owing to the lack of inexpensive and commercially-available f_H loggers designed for use in fish. Moreover, the technology that has been used has often been fraught with technical difficulties that likely discouraged wide-scale use. Among the few studies that have been published, most have used custom-designed devices. Custom-built electronic tags are almost necessarily more expensive to produce and can, in some cases, be less reliable, often requiring multiple iterations of field validation and tag refinement. The first publications arising from f_H loggers simply reported that such an approach was possible based on 3–4 fish implanted and held for short periods in aquaria (Kojima et al., 2003; Campbell et al., 2005). More importantly, cost-limitations and other logistical constraints have precluded large-scale release of fish equipped with f_H loggers—all of the papers published to date report on fish confined in artificial enclosures (e.g., bluefin tuna in large net pens; Clark et al., 2008). In other taxa, f_H loggers have been used more commonly in animals at liberty in the wild (e.g., seabirds—Bevan et al., 1997; Green et al., 2001; Weimerskirch et al., 2002; marine mammals—Andrews et al., 1997; Hindell and Lea, 1998; marine iguanas—Butler et al., 2002). The few examples that do exist in fish show the promise of this technology. Clark et al. (2010) were able to use a swim-tunnel respirometer to calibrate f_H output from a custom-built data logger with oxygen consumption in sockeye salmon. The same tags were also used to compare patterns in f_H between male and female sockeye salmon undergoing spawning activity (Clark et al., 2009) and to understand physiological recovery after simulated fisheries-capture in coho salmon (*O. kisutch*; Donaldson et al., 2010) and how f_H recovery is modulated by temperature (Raby et al., 2015). Makiguchi et al. (2009) used f_H loggers to show that chum salmon experience a temporary (~5–7 s) cardiac arrest during spawning, at the moment of gamete release.

2.4.2. Heart rate transmitters

Heart rate (ECG) transmitters were among the first physiological telemetry devices to be developed and used on fish in the field (Lucas et al., 1993). The earliest devices were based on radio telemetry platforms (Lonsdale, 1969) with acoustic ECG transmitters available several years later (Wardle and Kanwisher, 1973; Young, 1977). Early work focused on proof of concept and technical developments but by the late 1970s f_H telemetry was being used to address energetics questions in the field. For example, Priede (1978) used acoustic ECG transmitters to characterize diel patterns in f_H in an effort to understand biological rhythms in wild fish. Several years later, Lucas et al. (1991) used acoustic transmitters to quantify field metabolic rate and feeding in northern pike. A radio platform was then used to measure ECG in free swimming Atlantic salmon during spawning to examine sex-specific energy expenditure and f_H variability (Altimiras et al., 1996). Application of heart rate telemetry to more applied problems occurred later with a focus on quantifying the effects of recreational catch-and-release fishing on wild fish (Anderson et al., 1998).

2.5. Fine-scale fish positioning

Conventional telemetry tracking methods (i.e., positioning transmitter-equipped fish successively through time via manual tracking with a receiving unit) are useful for characterizing general movement patterns on time scales ranging from diel to seasonal,

but fail to provide adequate spatio-temporal resolution (e.g., variation in horizontal swimming path curvatures and velocity changes over time) for reliable use in estimating energy use. Moreover, estimates of distances traveled over time when conducting manual tracking will always be minimum estimates, and so estimates of swimming speed and associated metabolic costs of activity will also be conservative (e.g., McCleave and Horrall, 1970; Young et al., 1972; Løkkeborg et al., 2002; Cooke et al., 2001).

The precision and frequency of position estimates (or fixes) strongly influences the accuracy of swimming speed estimates (Hanson et al., 2007) so decreased fix intervals may be desirable. This can be accomplished by using passive telemetry systems (typically acoustic telemetry) that monitor fish position over finer spatio-temporal scales. These systems use overlapping acoustic detection ranges of three or more receivers to calculate positions in two or three dimensions via hyperbolic positioning (See Niezgoda et al., 2002 for details). Successive relocations provide high-precision tracks, increasingly near the sub-meter accuracy required to resolve localized activity (e.g., Niezgoda et al., 2002; Cooke et al., 2005; Espinoza et al., 2011; Huveneers et al., 2013). Theoretically these data can generate meaningful estimates of energy use, although to our knowledge there are no examples of papers in which positional data from a fine-scale fixed acoustic telemetry array have been used to generate information that was directly used as an estimate of some aspect of fish energetics, as opposed to simply making comparisons of relative activity levels (but see Semmens et al., 2013 for some preliminary attempts with great white sharks). For fish, neither radio telemetry nor satellite tags (including Fast Lock GPS) afford the same opportunities for fine-scale two-dimensional positioning as is possible with acoustic telemetry (Cooke et al., 2012a). There is however, potential to combine techniques (e.g., fine-scale acoustic telemetry array with use of acoustic accelerometer transmitters) to generate spatially explicit estimates of energy expenditure (e.g., Burnett et al., 2014), but examples of such work remain rare.

2.6. Other electronic tagging options

There are a number of additional electronic tagging tools that can be used to study the energetics of free-swimming fish although none have (yet) become as popular as the methods discussed above. The first attempt to correlate tail-beat frequency to ultrasonic telemetry signals was based on variations in continuous wave signals resulting from the undulations of the body and tail (Doppler effect) (Stasko and Horrall, 1976). This approach has not been widely adopted. Early attempts to measure tail-beat frequency directly using radio telemetry (Ross et al., 1981; Johnstone et al., 1992) were apparently successful, but they have not become commercially available. Similar developments with acoustic telemetry where a transmitter emits a signal with every lateral tail-beat have also failed to be widely adopted (Lowe et al., 1998). More recently, researchers have explored pressure-differential sensors capable of estimating energy output through the frequency and amplitude of tail-beats (Webber et al., 2001). Such sensors need to be mounted externally with the sensor placed near the caudal peduncle (to record maximum amplitude), which makes long-term deployments difficult. Differential pressure sensors have also been used to quantify ventilation rate by measuring opercular differential pressures (Dalla Valle et al., 2003).

Some researchers have attached speed-sensing transmitters to fish that use either a propeller or some form of a paddle-wheel style speed sensor often equipped with a magnet to quantify revolution speed (Block et al., 1992; Sundström and Gruber, 1998; Tanaka et al., 2001; Kawabe et al., 2004; Nakamura et al., 2011). Such devices can be attached to fish externally but paddle wheels and propellers can become stuck. Because of the velocity at which these tags initiate wheel movement is relatively high, they tend to be used on large, fast-swimming species (but see Watanabe et al., 2015 for example spanning taxa with diverse swimming abilities). Yet, a consistent problem with all speed-

sensing devices is that they tend to overestimate swimming speed and energy expenditure due to fish gliding and may also be influenced by water-current speed and direction (Brill et al., 1993). Despite the “simplicity” of these devices, their inherent challenges have delayed their broad adoption. Propellor-style sensors are incorporated into commercially-produced loggers from Little Leonardo from Japan (see Kawabe et al., 2004; Nakamura et al., 2011).

One of the more recent innovations is the development of a fully implantable blood flow radio telemetry system which allows simultaneous measurements of blood flow and temperature (Axelsson et al., 2007). Gräns et al. (2009, 2010) implanted the devices in adult green sturgeon *Acipenser medirostris* and obtained the first recordings of blood flow from free-swimming, untethered fish. The researchers measured blood flow in the ventral aorta (enabling them to calculate cardiac output) as well as the celiacomesenteric artery (as a measure of gastrointestinal blood flow). However, the application of such devices requires specialized surgical training and extensive knowledge of the anatomy and cardiovascular physiology of fish so it is unlikely that these devices will be widely embraced by fish ecologists, even though they will likely find application in the study of fundamental animal biology.

Other types of electronic tagging tools with potential relevance to fish energetics are those devices that incorporate image capture (either video or stills). The advent of tools such as the Critter-Cam (Marshall, 1998), the Little Leonardo camera logger (Kudo et al., 2007;) and waterproof action cameras (Struthers et al., 2015) provide opportunities for recoding and logging images that can be used to quantify tailbeats or feeding events (see Moll et al., 2007 for a review). There have been some attempts to relay images via remote means in aquatic systems but transmission distances are severely limited (Moll et al., 2007). Image capture devices are still relatively large and therefore limited to larger fishes (Struthers et al., 2015). One of the best examples of using cameras on fish involved deployments on ocean sunfish (*Mola mola*; see Nakamura et al., 2015).

Sensors that measure the internal milieu of fish (e.g., pH, metabolites; reviewed in Cooke et al., 2004a) are becoming more widely used in larger animals owing to biomedical advances although there are still relatively few examples using wild fish.

3. Assembling bioenergetics models from remotely-collected data

Obtaining field-based estimates of the metabolic costs of maintenance (SMR), activity (i.e., locomotion), and postprandial processes (specific dynamic action; SDA) as well as energy intake (feeding), excretion and conversion to somatic growth or reproductive investment each present their own challenges. The life histories of fishes are incredibly diverse and encompass all ecotypes from grazing herbivores to ambush piscivores to pelagic carnivores. This diversity necessitates customized approaches to quantifying field energetics through the use of electronic tagging, not least because of the vast differences in activity levels required by fishes in order to obtain food. For example, the energy budgets of ambush predators may only be transiently influenced by activity, whereas activity may have a significant contribution to the energy budgets of pelagic predators. Below, we discuss some primary energetic states and modulators of metabolism, along with other aspects of a generalized bioenergetics model (see Fig. 1) with a goal to highlight how tagging technologies can be utilised to estimate energy usage patterns of fish at liberty in the wild. Where possible, we attempt to identify exemplary studies in which electronic tagging techniques have been used successfully. In other cases, the examples we provide are conceptual suggestions and require further technological development and user creativity along with appropriate validation.

3.1. Standard/resting metabolism

Considering that the within-species variation in SMR is largely controlled by temperature and body size (Clarke and Johnston, 1999), it is

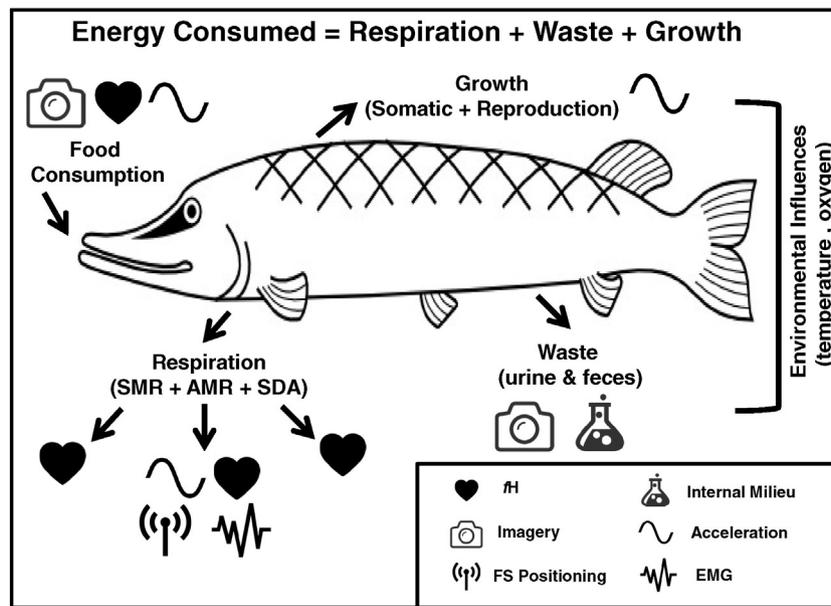


Fig 1. The generalized fish bioenergetics model with proposed biotelemetry and biologging tools that can (or could) be used to resolve each component of the model (indicated by different symbols, see legend). Acronyms include standard metabolic rate (SMR), active metabolic rate (AMR), and specific dynamic action (SDA).

possible that a tag-borne temperature sensor could be used to assign time-specific SMR to an animal based on laboratory-derived relationships (e.g., [Briggs and Post, 1997](#); [Halsey and White, 2010](#); [Hasler et al., 2012](#)). Best practices for quantifying SMR in fish in the laboratory (i.e., using respirometry) have most recently been described by [Clark et al. \(2013b\)](#) and by [Chabot et al. \(2016\)](#). To obtain field-based measurements of temperature, there are several commercially-available products that can be attached externally or implanted within the body cavity, including transmitters (e.g., [Carey et al., 1982](#)) and thermal loggers that in some cases can be relatively inexpensive (e.g., [Donaldson et al., 2009](#)). Although it may be argued that it is possible to estimate SMR based on temperature and body size alone, inter-individual differences in SMR can be significant (see [Burton et al., 2011](#); [Norin et al., 2015](#)) and it is important to verify activity levels and digestive status to ensure the assumptions of SMR are met. Using tagging technologies to further explore whether inter-individual differences in field-based SMR can predict differences in activity, behaviour, or habitat use could provide fundamental insights into niche partitioning, life history theory, and evolutionary processes.

There have been few successes in estimating the metabolic rate of free-swimming fishes using heart rate tags (e.g., [Lucas et al., 1991](#); [Clark et al., 2010](#)), but true values of SMR require the animal to be in a resting and post-absorptive state, conditions that can be difficult to verify using heart rate measurements from free-living animals. Simultaneous and non-interrupted records of temperature, trial-axial acceleration, and heart rate could be used to assess whether a fish is in a resting state (e.g., [Clark et al., 2010](#)). An additional consideration is that there could be among-individual differences in the calibration between tag output (e.g., heart rate) and energy expenditure, even in a resting state, because of inter-individual differences in how heart rate interacts with cardiac stroke volume and tissue oxygen extraction to influence SMR. Tags that measure blood flow (e.g., cardiac output) could circumvent this issue, but such tags are not yet routinely available ([Gräns et al., 2009](#)).

3.2. Locomotor activity

Activity-related metabolism has frequently been assessed using biologging and biotelemetry (e.g., [Cooke et al., 2004b](#); [Semmens et al., 2013](#); [Wilson et al., 2014](#)), and this is partly due to the relative ease

with which activity costs can be assessed in the field using the tools currently available ([Halsey et al., 2011](#)). However, there is also empirical justification for a focus on generating estimates of activity costs in the wild. Whereas much of the variation in SMR and SDA arises from variables that can be controlled in the laboratory (e.g., meal size, temperature, body size), activity is presumably controlled primarily by cognitive-behavioural processes (at least in a proximate sense) that are likely significantly different in fish confined in aquaria compared to animals in the wild. Furthermore, there is evidence that activity costs can vary widely among locales (e.g., 0–40% of energy budget), and that this variation can have large effects on resultant growth rates and fitness ([Boisclair and Leggett, 1989](#); [Rennie et al., 2005](#)).

In cases where the output of an activity-related tag has been calibrated with oxygen consumption rates (and/or swimming speeds) using laboratory experiments ([Wilson et al., 2013](#)), field-based measurements could be used to improve the accuracy of bioenergetics models. Without a lab-based calibration of energy expenditure, field-based tag outputs can still be used to make within-individual comparisons across times, places, or temperatures, but cannot be directly used to provide estimates of energy budgets. Regardless, comparative work can have ecological or applied value. For example, EMG telemetry has been used to assess the effects of different hydropower management regimes on swimming activity of salmonids (e.g., [Hasler et al., 2012](#); [Taylor et al., 2014](#)) and to estimate the energetic costs of migration ([Hinch et al., 1996](#)). Field-based estimates of activity costs can be easier obtained using accelerometry (e.g., [Burnett et al., 2014](#)) than with EMG-telemetry because small between-fish differences in electrode placement during EMG surgery can create major differences in tag outputs. This means it is especially important that individuals surgically-implanted with EMG transmitters are tested in a swim tunnel respirometer before release to ensure robust field-based estimates of energy expenditure ([Miyoshi et al., 2014](#)).

An underlying issue with all of the remote options for studying locomotor activity is the inability to directly quantify the anaerobic costs of swimming. Anaerobiosis and the associated exhaustive post-exercise oxygen consumption, represents a significant energetic cost so failure to quantify it brings uncertainty to bioenergetics modeling. Some authors have simply applied an anaerobic tax (e.g., [Hinch and Rand, 1998](#)). Combining direct measures of locomotor activity with direct measures of metabolism (e.g., through f_{H}) could address this issue.

3.3. Feeding and postprandial processes

While much focus has been placed on the development and application of methods for estimating energy expenditure in fish, energy acquisition is another important aspect of behavioural and energetic ecology and has important implications for bioenergetics models (Boisclair and Leggett, 1989). In partially-endothemic fishes (i.e., Scombroidei teleosts and Lamnidae sharks), thermal loggers can be used to measure the heat increment of feeding, which is highly correlated to the energetic value of the meal (Bestley et al., 2008; Clark et al., 2008; Whitlock et al., 2013). However, most fish are fully-ectothermic, precluding the use of this method. Foraging behaviours can also be identified using acceleration biologgers. For example, Broell et al. (2013) identified feeding strikes in an ambush predator (great sculpin, *Myoxocephalus polyacanthocephalus*) using algorithms based on characteristics of the acceleration signals from tri-axial ABs and verified video observations. Brownscombe et al. (2014) also used tri-axial acceleration biologgers to quantify foraging behaviour in bonefish (*A. vulpes*) in a wetland mesocosm using classification tree algorithms, which enabled identification of characteristic changes in body movement and pitch associated with benthic foraging. Integrating gyroscope sensors along with accelerometers, Kawabata et al. (2014) were able to identify foraging behaviour in white-streaked grouper (*Epinephelus ongus*), as well as which type of prey item (crabs or fish) was being preyed upon. Importantly, Kawabata et al. (2014) and Broell et al. (2013) emphasize the similarity between burst swimming related to foraging and that of predator evasion. Indeed, this makes identifying foraging behaviour challenging (O'Toole et al., 2010). Combining a gyroscope sensor with an accelerometer can offer greater behavioural detail but significantly reduces battery life and deployment duration, as well as adding mass to the tag. Due to limitations with obtaining data from ABs, no studies of which we are aware have quantified foraging behaviour in the wild using these tags.

Recent advances in accelerometer transmitters are making them a more functional tool with which to remotely quantify behaviour in fish. de Almeida et al. (2013) examined predatory feeding behaviour in the wild using accelerometer transmitters ('AccelTag', Thelma Biotel, Norway). AccelTag summarises acceleration data based on user input about the acceleration properties of behavioural events, (e.g., feeding, mating) based on tests using an accelerometer logger, with the data validated using direct observations of the behaviours. The AccelTag is then programmed with algorithms, which categorise the acceleration data (measured on the x, z and y axes at 20 Hz) into different behavioural events. The AccelTag then reports only the number of times the particular behaviour was recorded per pre-defined period (e.g., 1 h). Although this technology is still in its infancy, it was able to be used to define predatory (and other) behaviours in the Lusitanian toadfish *Halobatrachus didactylus*. These tags combine the advantages of ABs and activity tags because they are capable of recording fine-scale behaviours (i.e., beyond a generic assessment of activity levels) but only store and transmit the number of these events and provide no raw data. At ~30 days, the AccelTag life span is between that of a data logger and standard accelerometer transmitters.

Even though acceleration tags can be used to identify foraging events or searching (e.g., yo-yo dives of sharks; Losilevskii et al., 2012), it is difficult to distinguish between successful and unsuccessful foraging events (Brownscombe et al., 2014). Therefore, while data on foraging behaviour are relevant to behavioural ecology, it is still challenging to use acceleration data to estimate energy gain for the purpose of parameterizing bioenergetics models. Future research could attempt to distinguish between successful and unsuccessful events analytically, or by separately generating estimates of foraging efficiency. It may also be possible to incorporate imaging devices (in transmitters or loggers) to obtain visual confirmation of prey type when water clarity or light levels are sufficient for image capture. Heithaus et al. (2002) deployed Critter-Cams on adult tiger sharks to record foraging activity on video. More recently, Nakamura et al. (2015) used small cameras equipped

with lights on ocean sunfish to document feeding on siphonophores in 50 to 200 m of depth including at night. The same animals also had accelerometer loggers with provided opportunities to identify feeding-specific acceleration signatures. In marine mammals, researchers have extended the concept to estimating prey profitability and energy intake via image capture (e.g., Bowen et al., 2002), something that may be possible in fish when image capture tools are further reduced in size.

Postprandial processes (i.e., SDA) following a moderate-sized meal typically result in a several-fold increase in metabolic rate above SMR (at the peak of SDA; Secor, 2009), which can last for 1–390 h (Secor, 2009)—a function primarily of meal mass, meal energy content, and body temperature. Yet, similar to SMR, SDA is very difficult to quantify remotely and thus few studies have attempted to do so, with a notable exception being bluefin tunas due to their clear postprandial thermal increment in the viscera that mirrors metabolic rate (Bestley et al., 2008; Clark et al., 2010; Whitlock et al., 2013). Remote assessments of SDA have the potential to be tremendously valuable to ecology because SDA is closely tied to the energy content of food intake (Secor, 2009). Thus, quantifying SDA is one possible avenue to remotely estimate food consumption rates in free-roaming fish (Lucas and Armstrong, 1991). Because any rise in metabolic rate usually creates the need for increased cardiac output, electronic tags that record cardiac output or heart rate can potentially be used to quantify SDA. The problem one encounters is that it can be difficult to assign a rise in heart rate to SDA with confidence, without other accompanying information, because heart rate elevations can be caused by several factors such as activity and metabolic recovery (Clark et al., 2010; Donaldson et al., 2010; Raby et al., 2015). SDA has been monitored using heart rate loggers in free-swimming bluefin tuna in sea pens such that feeding events could be visually observed (Clark et al., 2008). The situation becomes more complicated in wild, freely-foraging tunas, but techniques have been devised to utilise the visceral thermal increment for estimates of SDA (Whitlock et al., 2013).

Perhaps the strongest available approach is to use a multi-sensor tag that combines temperature, tri-axial acceleration, and heart rate, and to make the assumption that any rise in heart rate above baseline not attributable to activity can be attributed to SDA. Lucas et al. (1991) used a similar approach in a study of three northern pike (*Esox lucius*) that were equipped with an ECG radio transmitter, assigning elevations in heart rate to SDA if the animal did not appear to be moving based on positional data. This approach could be subject to large error because metabolic rate can be elevated above SMR in the apparent absence of locomotion or digestion (e.g., during excess post-exercise oxygen consumption [EPOC] after brief anaerobic swimming, during wound healing, if the animal is in a diseased or reproductively mature state, or because of elevations in stress hormones). Moreover, heart rate appears only weakly related to metabolic rate in some cases (e.g., Scharold and Gruber, 1991; Thorarensen et al., 1996), presumably because those species modulate cardiac output primarily using changes in stroke volume rather than heart rate (few tagging technologies exist that quantify both; Gräns et al., 2009). For these reasons, species-specific laboratory evaluations of relationships between heart rate, oxygen consumption rate, and food intake should be developed prior to field applications (Lucas and Armstrong, 1991).

While tags do exist that monitor heart rate, temperature, and locomotory activity, battery or memory limitations generally require periodic rather than continuous sampling (e.g., 10 s of data sampled at 5–10 min intervals; Clark et al., 2008, 2010; Donaldson et al., 2010). A limitation with this approach is that most instances of brief, anaerobic swimming activity will be missed, yet may still be detected at some level due to delayed effects on metabolic rate via EPOC. In studies of field energetics where SDA is not being quantified, an approach that has been used to "solve" the SDA part of the bioenergetics equation is to assume some level of SDA-related expenditure at all times (i.e., adding an SDA value to SMR; Halsey and White, 2010), based on assumptions about minimum food intake

and laboratory-based relationships between temperature, meal size, and SDA. An alternate physiological proxy for energy expenditure during SDA is intestinal blood flow, but some evidence suggests this metric can be affected by environmental disturbances (Eliason et al., 2008), meaning that like heart rate, it may not be perfectly related to SDA. More importantly, intestinal blood flow has typically only been measured in animals tethered to recording equipment in the laboratory (e.g., Thorarensen and Farrell, 2006), although some telemetered data do exist (Gräns et al., 2010). A final approach would be to record feeding events via some other mechanism (e.g., Critter-Cams, tri-axial accelerometry, see above) and then to estimate meal size and the resultant SDA based on laboratory-derived relationships between meal size and temperature. In the absence of visual verification of the food (e.g., with Critter-Cams or the Little Leonardo camera), this approach would rely on guessing the size and type of food consumed, both of which can have significant impacts on the magnitude of the SDA response. Another avenue for investigating food consumption via gastically-implanted pH tags (e.g., Papastamatiou et al., 2008; Meyer and Holland, 2012), although this technology has not yet been widely adopted.

3.4. Waste

Faecal and urine losses give an indication of how much of the nutritional content of the food has been absorbed by the fish. If it is possible to measure faecal loss, the time between ingestion to faecal loss could provide valuable information on transit time. Obtaining information on waste in fish remotely is challenging, has not been achieved in free-swimming fish in the wild (to our knowledge), and will likely require a new suite of sensors (e.g., pH).

Sensors that measure the internal milieu such as changes in pH or ammonia could provide information on urine excretion. Anal muscular activity could also be measured with EMG sensors – however, this would prove highly complicated in the field given size constraints and the need for attachment accuracy. Accelerometer sensors are unlikely to be of use, since even if they are correctly placed and sufficiently sensitive to measure changes in anal activity, it will be difficult to distinguish such movements from irritation, reproduction, or movement due to loose attachment.

Evidently, the current technological challenges make it difficult to obtain direct measurement of faecal and urine losses. However, accelerometers and gyroscopes could provide an indirect method for estimating discharge: the time at prey ingestion (e.g., Broell et al., 2013; Brownscombe et al., 2014) and prey type (Kawabata et al., 2014, see above) combined with a species-, prey-, and temperature-specific evacuation term could deliver indirect estimates of faecal loss and offer a feasible solution to estimating the waste term in the bioenergetics equation. Conceivably one could use measures of ammonia in vasculature near the gills to quantify gill excretion of waste.

3.5. Growth

Growth variation in fishes is typically inferred from size-at-time (age) which, in many cases, requires lethal (e.g., to obtain otoliths or other calcified structures) or repeated sampling of marked individuals (see Quist et al., 2012). This method cannot resolve individual growth that is a function of temperature as the fish moves through its temperature-varying environment (Neuheimer and Taggart, 2007). The idea of measuring fish growth remotely is an interesting one that is not intuitive but has a fascinating theoretical foundation. Onboard micro-scale accelerometry can provide an *in situ* estimate of length-at-time, if fish acceleration, within species, is primarily a function of size. The theoretical relationship between size and acceleration in fish has long been considered (Bainbridge, 1958; Wardle, 1975; Daniel and Webb, 1987) and acceleration during steady and unsteady swimming has now been linked to increases in body size.

In a recent paper, Broell and Taggart (2015) suggest that size can be estimated based on lateral acceleration records using tail beat frequency as a predictor. Given that swimming speed and size are independent, tail beat frequency (estimated from acceleration values) during steady swimming inversely relates to size-at-time. In cases where maximum swimming speed is proportional to length, maximum sustained tail beat frequency could be used as an alternate predictor, since it relates to size independently of swimming speed. This method has realistic potential for field applications to measure size-at-time and over time, growth rate, given its high accuracy (as low as 4% uncertainty) and technological feasibility. It requires low (~15 Hz) sampling frequency, and a small number of periodic samples over time (to conserve battery power), which is essential for long-term growth studies.

Maximum acceleration (A_{max}) (Webb, 1978; Domenici and Blake, 1997) and other parameters measured during burst acceleration (e.g., standard deviation of acceleration; Broell et al., 2013, unpublished data) also relate to size and could therefore be used as estimates of size. However, since these movements begin and end within an extremely short period of time (<1 s) they require high sampling frequency (>50 Hz, Broell et al., 2013) and continuous sampling, which (currently) limits battery life to an extent that deployment durations would be insufficient for studies of growth in most cases. It may also be possible to assess growth based on changes in heart rate or cardiac output associated with allometric scaling (e.g., Clark and Farrell, 2011).

3.6. Reproductive investment

Remote identification of the behaviours associated with actual spawning events (e.g., quivering, circling, rolling) is quite feasible (Healey et al., 2003; Whitney et al., 2010), and discussed above (see Section 3.2), but estimating the energetic cost of reproductive investment presents major challenges. Given that somatic growth decreases at maturity when most energy is invested into reproductive growth (Roff, 1983), estimates of size (and growth rate; as outlined above) could be used to remotely determine the size- and age-at-maturity. For example, when age-at-maturity is reached, dominant tail beat frequency (e.g., measured with accelerometers as outlined in Broell and Taggart, 2015) will remain nearly constant over time, indicating constant length and that maturity is reached. Age-at-maturity could then be used to measure the start of somatic growth of the gonads.

For species in which reproductive growth (e.g., gonad development) results in increase in weight, it may be possible to differentiate pre- (increase in length and weight) and post-maturity growth (increase in weight, not length) using accelerometers. Experimental data on the differences in acceleration and/or locomotory parameters associated with changes in weight from mature fish of the same length would allow the calibration between acceleration and reproductive growth. Such differences are expected since swimming efficiency decreases in fish with an increase in the mass:length ratio (Broell and Taggart, 2015). These parameters could then be used to estimate how much energy is allocated to reproductive growth post-maturity although that may not be feasible for capital breeders that transfer somatic energy to gonad development. For species in which significant weight gain does not occur in the lead-up to reproduction, measuring reproductive growth using acceleration tags would be challenging.

A multi-parameter model combining acceleration records during steady-swimming (e.g., maximum or steady tail beat frequency) and unsteady swimming (e.g., A_{max}) in conjunction with the thermal integral (Neuheimer and Taggart, 2007) and pre- and post-maturity changes in weight could likely provide an estimate of somatic growth and reproductive growth. Combining the knowledge of the initial fish size at release with the estimates of growth potential and age-at-maturity could further improve the potential to remotely estimate changes in size over time by using a multi-parameter scaling model in a state-space framework. Notably, reproductive investment is an energetic

cost that is independent of body movement, and so devices that measure heart rate and/or cardiac output should provide insight into the energy expended on reproductive maturation. It may also be possible to place pressure sensors (e.g., near the gonads (especially in female fish) that register how full the abdominal cavity is getting (internal walls being pushed on by a growing gonads) to reflect gonad size. Such an approach would require extensive laboratory experiments to confirm the relationship between pressure measures and gonad mass. If it were possible to relate acceleration profiles associated with gamete deposition to actual quantities of sperm or eggs, it may be possible to infer investment (forthcoming paper on the topic; Trevor Pitcher, Univ of Windsor, Personal Communication).

3.7. Environmental influences

Environmental temperature has fundamental effects on each component of the bioenergetics equation for all ectotherms because of its direct effect on body temperature and the rate of biochemical reactions (Fry, 1971; Brett and Groves, 1979). Therefore, any robust effort to obtain remote measurements of energetics in fish should include simultaneous measurements of temperature, ideally measured using an animal-borne sensor. Alternatively, where high-resolution environmental temperature data are available and the thermal environment is relatively homogeneous, temperature may be estimated based on known animal positions without a requirement for a sensor in the body cavity of the fish. Temperature has more fundamental control over some aspects of energetics than others. For example, while food intake and resultant growth both may be affected by temperature, food intake can be dependent on food availability and foraging success, while growth can be affected by the amount of energy spent on locomotion. On the other hand, components like SMR are primarily under the control of temperature, and it can be defensible to use temperature alone (in combination with factors like body size and sex) to generate a field-based estimate, even though this approach does not constitute a remote measurement. Temperature could also be used to directly predict/estimate growth, if other components of the bioenergetics model are known based on remote measurement (e.g., SDA, SMR, activity). Perhaps one of the promising aspects of obtaining remote measurements for bioenergetics variables is that they could provide important insight into how temperature affects foraging success, activity, growth, and reproductive output—data that would be useful for predicting the effects of climatic change.

Water parameters other than temperature (e.g., levels of dissolved oxygen [see Coffey and Holland, 2015], carbon dioxide, or concentrations of contaminants) can modify the metabolism of fishes without necessarily affecting other variables like activity, thus leading to inconsistencies in tag-derived estimates of energetics variables. Given that a change in metabolism is often associated with a change in blood flow, heart rate and cardiac output sensors should help to decipher any impacts of water parameters on energy expenditure. Measurements of body movement (e.g., acceleration, EMG) may not provide an indication of environment-related changes in metabolism, although the inclusion of environmental sensing tags (e.g., to detect hypoxia) could help to circumvent this issue and allow a lab-derived calibration to be used dynamically as environmental conditions change.

4. Integration and bioenergetics—more than a sum of parts

With the advent of diverse biologging and biotelemetry tools, estimating the locomotory activity component of the bioenergetics budget has become relatively simple. Although an important component of the bioenergetics budget (Boisclair and Leggett, 1989), it is only one component. Researchers have tried for decades to measure other components (e.g., SDA, feeding, SMR) but with inconsistent results. Indeed, some aspects of bioenergetics are immensely challenging to study in free-swimming wild fish. For example, how much urine does a fish pass in

a day? Or how much energy does it excrete as faecal material? Future innovations in sensor development related to changes in chemistry or flow measurement may be needed. In large animals, an image capture device could be placed near the anus. Determining how a fish allocates surplus energy to somatic growth and reproduction is something that is not intuitively practical to measure remotely. Nevertheless, a better understanding of biomechanics and scaling rules is opening doors for using accelerometry to remotely measure growth and reproductive investment. Although it may not be necessary (or possible) to make remote estimates for every part of the bioenergetics model in a given species, remote field-based measurements of a given component can facilitate a) accurate values for use in modeling exercises, and b) ‘solving’ for other parts of the equation.

Today the electronic tagging toolbox is bigger than ever (see Fig. 2) and unlike in decades past, there is an increasingly large assortment of devices that are available from commercial manufacturers (e.g., Cefas, Biologging Solutions, Maritime bioLoggers, Gulf Coast Data Concepts, Lotek Wireless, Vemco-Amarix, Thelma BioTel, Advanced Telemetry Systems, Little Leonardo, Wildlife Computers). Early developers and adopters of tagging technology for the study of fish energetics were (and still are to some extent) as much electronics technicians as they were biologists which led (and continues to lead) to a number of failures or “one-offs”. Those working at that frontier were nevertheless doing an important service to the scientific community even if the tags they developed did not provide a technically-reliable or commercially-viable tool at the time. Some devices, such as tags for measuring cardiac blood flow or electromyograms, require specialized training to attach to fish and therefore are less likely to be commercially-produced. And for nearly all electronic tag types, there is need for technically-challenging and labour-intensive calibration and validation in the laboratory, steps that must be taken seriously if one is to use the technology to remotely measure energy intake, use or waste.

Because electronic tagging studies can generate enormous datasets, it has become increasingly important to develop capacity for data management and analysis. Data interpretation must be performed with caution and with a strong understanding of organismal physiology and environmental relations. This is all to say that to study the energetics of fish in the wild is a multi-disciplinary enterprise that requires a research team with expertise in areas such as fish surgery, tracking, physiology, ecology, behaviour, and data analysis.

Future technological advancements in biotelemetry and biologging will surely involve novel sensors, smaller devices, longer battery life and higher capacity for data storage and transmission. There is also a need to address key issues such as how to quantify EPOC arising from anaerobiosis. Moreover, there are inherent challenges that exist with rapid transmission of data such that many of the current transmitting platforms average sensor data over relatively long (e.g., 3 to 20 s) time frames which reduces ability to detect biologically-meaningful activities and likely leads to underestimates of true energetic costs. The trade-off between having high-resolution logging data with the need to recover the tag versus having lower-resolution data but that is transmitted remotely is a reality for every biologging and biotelemetry study in fish. Moving forward we expect that the future will more likely involve a focus on integrating different existing sensor-types and methods to provide a more complete picture of fish bioenergetics. For example, Watanabe and Takahashi (2013) combined animal-borne video loggers with accelerometer loggers to assess variability in prey capture for Adélie penguins. One of the few fish example we are aware of is Clark et al. (2010) where the authors used simultaneous biologging of heart rate and acceleration to assess energy expenditure in sockeye salmon on spawning grounds. It is also possible to combine different sensors and approaches in different studies within a broader research program as has been done for Pacific salmon in the Fraser River of British Columbia (See Fig. 3). To date, most combined sensor packages/devices in fish have focused on environmental sensors (e.g., temperature and depth)

Device and/or Sensor Type	Year							
	1955	1965	1975	1985	1995	2005	2015	2025
EMG transmitter (locomotion)								
EMG transmitter (opercular/mandibular)								
Acceleration logger								
Acceleration transmitter								
HR logger								
HR transmitter								
Positional telemetry (coarse-scale)								
Positional telemetry (fine-scale)								
Blood flow transmitter								
Imagery logger/transmitter								
Multiple Devices and/or Sensors								

Fig. 2. Perceived relative popularity (based on literature, expertise of author team, and commercial availability) of different electronic device and/or sensor types used to assess the bioenergetics of wild fish. The blank (white) indicates little to no availability or use in a given technology where the darkest fill (black) indicates that a device is commercially available and has been broadly embraced by the research community. Shades in between indicate relative popularity.

coupled with a single energy-related sensor (e.g., acceleration; the Cefas loggers incorporate all three of these sensors) as opposed to multiple energy-related sensors.

Borrowing, extrapolating, or simply guessing the value of parameters is a reality in contemporary bioenergetics modeling (Ney, 1993). The techniques we outline here will allow the generation of real

measurements of many aspects of bioenergetics – from intake to use to allocation to waste. Given that energy is the fundamental currency of biology, refined techniques for making remote bioenergetics measurements will hopefully enable bioenergetics to become central to how we understand human impacts on wild fish in a drastically changing environment.



Fig. 3. Some of the biotelemetry and biologging techniques that have been used as part of a long-term integrated research program on the Pacific salmon of British Columbia (see Cooke et al., 2008 for summary). The research program spans fundamental understanding of animal–environment relationships and biological correlates of fitness to more applied aspects such as fisheries interactions, hydropower impacts and climate change (Cooke et al., 2012b). A) EMG telemetry has been used to track migratory adult salmon during their upriver migration and spawning to quantify energy use for inter-, sex-, and location-specific comparisons (e.g., Hinch et al., 1996; Hinch and Rand, 1998; Healey et al., 2003). B) Loggers with ECG and accelerations sensors have been used to quantify the energetic costs of spawning (Clark et al., 2010), fisheries interactions (Raby et al., 2015), and predator interactions (Donaldson et al., 2010). C) Most of the devices used for the study of the energetics of free-swimming fish require careful calibrations often involving swimming fish in respirometers (e.g., Wilson et al., 2013). D) Fish are tracked in the wild using manual tracking or fixed receiver stations. Photo Credits: A, B, D (Steven Cooke), C (Samantha Wilson).

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