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Activity and energetics of free-swimming fish: insights from electromyogram telemetry

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Abstract

Electromyogram (EMG) telemetry studies that involve remotely monitoring the locomotory activity and energetics of fish are contributing important information to the conservation and management of fisheries resources. Here, we outline the development of this rapidly evolving field and formulate the studies conducted that utilize this technology. To date, more than 60 studies have been conducted using EMG telemetry that spans 18 species. Several general trends were observed in the methodology of the studies that we have highlighted as standards that should be adopted associated with transmitter customization, electrode placement and surgical technique. Although numerous studies have been methodological, there are still some deficiencies in our basic understanding of issues such as the need for individual calibration and the method of reporting or transforming data. Increasingly, this technology is being applied to address issues in conservation, management and aquaculture production. At present, the technology has been most frequently applied to the study of animal activity or energetics and to migration. Several recent studies have also focused on addressing more basic questions in ecological and evolutionary biology (e.g. parental care dynamics) similar to the large body of literature that has been collected for other taxa (e.g. marine mammals, birds), using activity telemetry. Collectively, studies conducted using EMG telemetry have contributed important information on free-swimming fish that was previously difficult to obtain. EMG telemetry is particularly effective for examining behaviour at temporal and spatial scales that are difficult using other techniques. The development of an ultrasonic transmitter based on the same proven principles as those used in the current radio transmitter technology will permit studies in other environments (i.e. marine, brackish, deep water) and on different species of fish. We encourage the continued development and refinement of devices for monitoring the activity and energetics of free-swimming fish, and also encourage researchers to consider EMG telemetry as a tool for addressing questions that are not effectively answered with other techniques.

Keywords behaviour, energetics, locomotion, physiological telemetry, swimming activity

Introduction

Knowledge of the activity and energetics of free-swimming fish are desired goals of fisheries managers (Ney 1993), ecologists (Butler 1989; Nagy 1989; Kotrschal and Essler 1995; Lucas and Baras 2000) and aquaculturists (Baras and Lagardére 1995) in both the laboratory and the field environments. Activity and movement rates of fish provide direct information on the swimming behaviours and ecology of fish and are essential for food acquisition, predator avoidance and seasonal habitat shifts (Beamish 1978; Lucas and Baras 2000). Swimming requires the integrated function of many different body systems (Schreck 1990), and thus alterations in locomotory activity (i.e. depressed activity, hyperactivity) can serve as sensitive indicators of stress (Scherer 1992; Schreck *et al.* 1997; Cooke *et al.* 2000c). In addition, as locomotory activity represents one of the largest and most variable portion of a fish's energy budget (Boisclair and Leggett 1989), estimating the activity and energetics in free-swimming fish may permit the accurate derivation of energetics models (Brett and Groves 1979; Boisclair and Sirois 1993). However, fish pose several challenges to those interested in assessing these variables, especially in field settings (Lucas *et al.* 1993). Ideal approaches to data collection would be generally noninvasive and would permit evaluation of *in situ* conditions without repeatedly handling or terminally sampling individuals (see Cooke *et al.* 2002a). Conventional approaches used to assess the locomotory activity and energetics of free-ranging fish have included noninvasive videography (Hinch and Collins 1991; Trudel and Boisclair 1996) and locational telemetry (Diana 1983; Lucas and Baras 2000) or destructive proximate body composition analyses (Brett and Groves 1979). Some researchers have also used doubly labelled water to assess energy expenditure, but it has serious limitations because water flux in fish is too high to obtain detectable readings from recaptured fish that have been at liberty for sufficient time (see Nagy 1989). These approaches are undoubtedly useful, but have limitations in many situations that either make it difficult to obtain continuous time-series data or to collect data at appropriate temporal and spatial scales for detailed assessments of locomotory activity and energetics.

To remedy the difficulties in monitoring the behaviour and energetics of free-swimming fish, researchers have developed a series of physiological telemetry techniques (see Lucas *et al.* 1993). Although it is now possible to monitor a number of different variables, only electromyogram (EMG) locomotory activity telemetry has become well represented in fisheries research (e.g. Hinch *et al.* 1996; Briggs and Post 1997a; Cooke *et al.* 2002b). As these EMG telemetry studies have addressed many different objectives in a variety of disciplines (e.g. behavioural ecology, aquaculture), the literature base is somewhat diffuse. A comprehensive synthesis of existing EMG studies would be useful for individuals not familiar with this technology evaluating the appropriateness of this method for addressing their desired objectives. Furthermore, a synthesis would serve to provide researchers with information on the methodologies employed in existing studies and the diverse scenarios to which these techniques have been applied. A review could also serve to develop standardized techniques that would facilitate interstudy comparisons. Thus, the goal of this paper is to provide a comprehensive and detailed synthesis of the technical and methodological applications of EMG locomotory activity telemetry in fisheries science. In addition to reviewing past research on this topic, we also discuss the benefits and limitations of this technology and provide a prospectus for future research utilizing EMG telemetry.

Types of locomotory activity telemetry

There are a number of different telemetric methods for studying the activity and energetics of free-swimming fish. As telemetry of fish was reported for the first time in 1956 (Trefethen 1956), biotelemetry has become commonplace and is still expanding in popularity and use. Traditionally, conventional techniques that only locate individuals were employed. Conventional telemetry methods have been useful in determining positions and movements of individual fish, but these methods ignore movements in depth, horizontal swimming path curvatures and velocity changes over time. Estimated distances swum over time will always be minimum estimates, so estimates of swimming speed and associated metabolic costs of activity will also be conservative values (e.g. McCleave and Horrall 1970; Young *et al.* 1972; Løkkeborg *et al.* 2002). The precision and frequency of location measurements strongly influence the accuracy of swimming speed estimates, so decreased fix interval may be desirable. Using three-dimensional acoustic arrays, it is possible to obtain high-precision tracks, but not at the submeter accuracy required to resolve localized activity patterns (Løkkeborg *et al.* 2002). Recently, biotelemetry has developed into a variety of highly sophisticated techniques that measure and transfer wireless information from free-swimming fish on physiological variables such as heart rate, opercular rate and muscle activity.

Heart rate has been used as a correlate of activity by obtaining electrocardiograms (ECG) using telemetry methods (e.g. Lucas *et al.* 1991). However, heart rate in fish can be affected by stimuli other than exercise (e.g. Priede 1978) and may not always correlate well with the intensity of physical activity. Early attempts to measure tail-beat frequency using radio telemetry (Ross *et al.* 1981; Johnstone *et al.* 1992) were apparently successful, but they have not become readily available in the commercial market. 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 body and tail (Doppler effect) (Stasko and Horrall 1976). This approach has not been widely adopted. Some researchers have attached speed-sensing transmitters to fish. Block *et al.* (1992) measured speed using a velocity meter equipped with a plastic propeller containing a magnet that activated a reed switch that was trailed from a semirigid stock attached to the transmitter. A paddle-wheel-style acoustic activity transmitter was deployed by Sundström and Gruber (1998) on elasmobranchs. This device can be affixed quickly and calibrated in a respirometer, but occasionally the paddle wheel becomes stuck (which is a problem with all paddle wheels and propellers). In addition, the velocity at which these tags initiate wheel movement is relatively high, so these devices are currently most useful for large, fast-swimming species. Kawabe *et al.* (2003) and Tanaka *et al.* (2001) used archival transmitters to record two axis acceleration on Japanese flounder

(*Paralichthys olivaceus*;[1] Paralichthyidae) and chum salmon (*Oncorhynchus keta;* Salmonidae), respectively. This transmitter provided information on tail-beat frequency, and hence swimming speed, but as the data are not transmitted, and as the device is external, this type of transmitter may be severely limited in field settings. All speed-sensing devices may over-estimate swimming speed and energy expenditure because of fish gliding and may also be influenced by water-current speed and direction (Brill *et al.* 1993).

Two more recent developments, both of which are ultrasonic do show some promise for monitoring the activity of free-swimming fish. The first is a tail-beat transmitter that emits a signal with every lateral tail beat (Lowe *et al.* 1998). The second is a device that utilizes a pressure differential sensor capable of estimating energy output through the frequency and amplitude of tail beats (Webber *et al.* 2001). These devices are less invasive than current EMG technologies, but as they are generally externally mounted to place the sensor near the caudal penduncle (to record maximum amplitude), the monitoring duration is limited. At present, there are very few studies that are based upon these technologies. Although there are a multitude of techniques for assessing locomotory activity in free-swimming fish, all these techniques have significant limitations. Only transmitters that detect and transmit (using radio signals) EMGs produced in muscle activity of free-swimming fish have become common as a tool in fisheries research.

Development and description of EMG telemetry transmitters

Electromyograms are bioelectrical voltage changes that are roughly proportional to the degree and duration of muscle tension (Sullivan *et al.* 1963). Biochemical processes at the tissue level determine oxygen demands of muscular activity at any given temperature (Weatherley and Gill 1987). It is assumed that the EMG generated by a representative myomere will be highly correlated with the oxygen consumption that results from the activity of the entire myomere series (Weatherley *et al.* 1982; Weatherley and Gill 1987). The main swimming muscles in most fusiform fish are the axial muscles consisting of a bilaterally symmetrical series of myomeres (Bone 1978; Bone *et al.* 1978). Thus, in these fish, EMGs recorded from electrodes embedded into these muscles can be used as quantitative indicators of overall fish activity, and as a means of obtaining quantitative estimates of swimming speed or the metabolic costs of activity by calibrating EMGs to tail-beat rate, swimming speed or oxygen consumption within methodological constraints. In recent years, research on swimming kinematics has expanded to include fish with nonfusiform body forms such as the perciforms. In perciforme fishes, axial musculature may be less important at low swimming speeds, but crucial for generating high power for fast starts and high-speed swimming (Webb 1994). Fundamental understanding of swimming mode and muscle function in different types of fish is required to adequately implement and interpret EMG studies, but in general, relationships generated between axial EMG activity and swimming speed during forced swimming are rather strong for most species.

EMG activity can be measured in laboratory environments using hard-wired electromyography systems. Paired electrodes are placed in a single myomere and allow the detection, amplification, and subsequent recording of electropotentials (e.g. Loeb and Gans 1986). Hard-wired studies typically focus on understanding the fundamentals of muscle function and swimming performance. Although these studies have yielded a wealth of information, they are generally restricted to flumes, tanks or other confined laboratory conditions (e.g. Rome *et al.* 1992). Several researchers have used long electrode leads to quantify the spawning behaviour of chum salmon, but these fish remained tethered directly to a signal amplifier restricting mobility (e.g. Uematsu *et al.* 1980; Uematsu and Yamamori 1982). Because of the desire to monitor the activity of fish under unconstrained field settings, research began to develop technologies to facilitate the quantification of muscle activity in free-swimming fish using telemetry.

In the 1970s in Scotland, implanted extracellular electrodes linked to an externally attached ultrasonic transmitter were used to detect EMGs from the *m. adductor mandibulae* (muscle responsible for closing the mouth) of brown trout (Oswald 1978). By analysing the EMG signals transmitted, feeding was successfully distinguished from other types of activities, such as coughing. Tagged fish were released in a lake, and feeding activity and ventilatory rhythms were monitored from free-living fish for extended periods (Oswald 1978). A similar transmitter was implanted in the lateral musculature and used for continuous

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[1] Latin names for species used in this review are only included in this table. Species not listed here are presented with latin binomial and family.

monitoring of tail-beat rate from lake-dwelling brown trout (Ross *et al.* 1981). Subsequently, swimming speeds of the fish were calculated from the records of tail-beat rate, using a relationship developed by various authors for rainbow trout (Ross *et al.* 1981). Results showed that the fish rarely swam at speeds that would incur oxygen debt (Ross *et al.* 1981). Clear diurnal rhythms in fish activity were demonstrated in both studies (Oswald 1978; Ross *et al.* 1981).

At the same time as the Scottish researchers developed an EMG ultrasonic transmitter, Canadian researchers developed and tested techniques that utilized radio telemetry to transmit EMGs from free-swimming fish (Sayre 1978; Luke *et al.* 1979; Weatherley *et al.* 1980; Patch *et al.* 1981; Rogers *et al.* 1981). They were able to calibrate EMGs from rainbow trout to oxygen consumption in the laboratory and concluded that the good correlations between oxygen consumption and EMGs gave promise for more accurate determinations of fish standard metabolic rate than formerly had been possible (Weatherley *et al.* 1982). They also concluded that records of fish EMGs can be used as direct indices of activity without the need to translate them into energy units (Weatherley *et al.* 1982). This can be useful in attempts to identify the onset and intensity of aspects of annual activity regimes, such as spawning or changes in irritability associated with the presence of environmental toxicants (Weatherley *et al.* 1982). An attempt to correlate EMGs recorded from *levator arcus palatini*, a small muscle involved in the opening of the gill operculum, with oxygen consumption in rainbow trout was effective for fish under forced-swimming conditions, but not when swimming spontaneously (Rogers and Weatherley 1983). EMG records obtained from rainbow trout released into a small lake and monitored for up to 4 weeks indicated a fairly regular pattern of elevated mid-day activity contrasting with periods of relative quiescence during the evening and morning (Rogers *et al.* 1984).

The Canadian researchers were not satisfied with the technical solution of the previous EMG transmitters and, together with electronic engineers from Lotek Engineering Inc. (now Lotek Wireless Inc.), developed the only EMG transmitter that has been commercially available until today (see Kaseloo *et al.* 1992; Thorstad *et al.* 1999; Lotek Wireless, EMG Transmitter). The current EMG transmitter consists of an epoxy-coated transmitter package (13 mm (diameter) × 51 mm (length), weight 18.0 g in air), two paired, Teflon-coated stainless steel electrode wires and a whip antenna. The two electrodes of the surgically implanted EMG transmitter are implanted in musculature (Fig. 1). EMGs are transmitted as radio pulses, with the intensity of muscular activity determining the intervals between pulses (Kaseloo *et al.* 1992). Bioelectric potentials exceeding 1–2 µV adjacent to electrodes is detected by the transmitter, integrated, amplified (×27 000) and stored in a capacitor. A precision half-wave rectifier processed input EMGs within the bandwidth of 30–350 Hz. These electropotential events are accumulated until they reach a factory-determined threshold, which when exceeded emits a radio signal. Once the radio signal is emitted, the power capacity reverts back to zero and the process repeats itself. The transmitters also have a factory- set background level of energy accumulation in the capacitor to ensure that the researcher can still locate the fish and transmitter when the fish is immobile or dead. The background level of capacitor energy accumulation that provides resting pulse rate varies between transmitters, likely reflecting variation between individual component characteristics. The time between emitted radio signals is recorded by the EMG receiver. The frequency of signal emission is dependent upon the level of muscle activity, with more activity resulting of the more rapid attainment of capacitance and hence more frequent transmission of signals. As these signals are received more frequently, the interval between

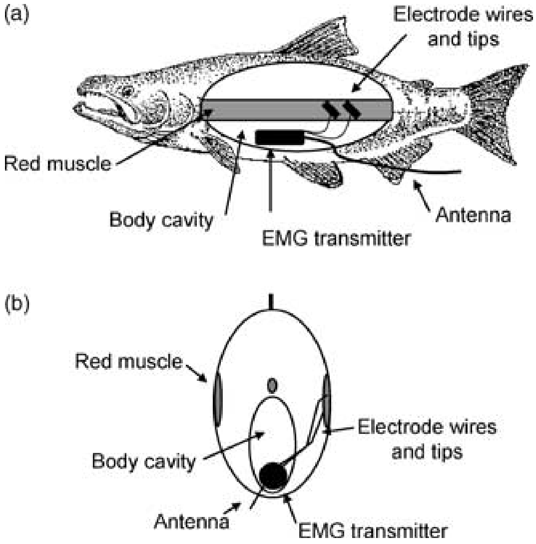

Figure 1 Schematic diagram of EMG transmitter location in a generic salmonid including (a) lateral and (b) cross-sectional perspectives. The transmitter is not drawn to scale.

successive pulses decreases. This results in an inverse relationship between fish locomotory activity and pulse interval. This design of EMG transmitter does generate some problems as the values derived represent a 'black box'. If transmitter output was directly proportional to the sum of the time-sampled voltage amplitudes and expressed as a sum of voltages, and was proportional to the pulse interval, one could use a voltage spike generator to calibrate the transmitters. Instead, the inclusion of background energy contributing to the capacitor precludes the determination of these more biologically meaningful values.

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-s time period. These individual samples are summed and stored until the end of the 3-s 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 these differences in how signals are transmitted, the coded nature of the transmitters permits multiple transmitters to be monitored simultaneously on the same frequency. These transmitters are still in the beta testing stage and yet to be represented in the literature. For this reason, the focus of this review is on the current EMG transmitter that will continue to be commercially available for the foreseeable future. It is important to note that the coded EMG transmitter actually serves as more of a 'black box' value generator than does the current EMG transmitter and so may not represent the type of advancement that would aid in the generation of more biologically relevant signals.

VHF radio transmitters cannot be used in the marine or brackish environments because the radio signal is rapidly attenuated by salt water. Similarly, deep freshwater systems also result in major signal attenuation. The EMG transmitters described above is thus limited to shallow freshwater environments. No acoustic EMG transmitters are commercially available at present, but in the USA, some work has been done on developing and testing an acoustic EMG transmitter (Dewar *et al.* 1999). Their aim is to develop a transmitter that more precisely replicates the complex character of the EMG by monitoring the full EMG waveform (Dewar *et al.* 1999). That level of activity would be useful for studies of muscle physiology, but is less relevant to information on fish activity and energetics. Nonetheless, the function of the transmitter described by Dewar *et al.* (1999) does provide a clearer measure of the biological characteristic being monitored and, as such, serves a less of a 'black box' than the Lotek EMG transmitter. At present, this is the only published study using this technology and the devices are not commercially available.

Methodological issues

Since the initial development of EMG telemetry, this technology has been used in many studies. Below is a synthesis of 65 existing EMG telemetry studies that make use of the commercially available Lotek EMG transmitter (Table 1). The first study utilizing the commercially available EMG transmitter was McKinley and Power (1992). After that study, there was a period of several years when no additional work was published. However, beginning in 1996, there has been a rather steady publication rate of studies utilizing EMG transmitters (Fig. 2). Below, we first discuss methodological issues associated with the customization of the transmitter, the surgical implantation, calibration and data analysis. After that, we provide an overview of the range of studies to which EMG telemetry has been applied. To locate existing EMG telemetry studies, we utilized several literature search engines including Fish and Fisheries Worldwide, Aquatic Sciences and Fisheries Abstracts and Web of Science. We also searched the internet, dissertation abstracts and conference abstracts. We also used our network of contacts utilizing EMG telemetry to find unpublished data or grey literature. In instances where data were reported in both thesis and publication form, we combined data as appropriate. We queried authors with unpublished data with a series of questions that permitted us to extract desired information. When studies incorporated clearly different phases or components that utilized different individual fish, we included the data for each of the two distinct phases. When calculating summary statistics, repetitive information from different phases of the same study were not counted on more than one occasion except where relevant. Some studies did not report all details, so in many cases the total sample size is less than the total number of studies ($N = 65$) that we examined.

Transmitter customization

There has been some variation among studies with the types of electrodes used for detecting EMG

Table 1 EMG telemetry studies reviewed in this paper.

Citation	Common name	Latin name	Family	Study application
Beddow and McKinley (1998)	Atlantic salmon	*Salmo salar*	Salmonidae	Methodological
Beddow and McKinley (1999)	Atlantic salmon	*Salmo salar*	Salmonidae	Methodological
Booth *et al.* (1997)	Atlantic salmon	*Salmo salar*	Salmonidae	Methodological
Booth *et al.* (1997)	Atlantic salmon	*Salmo salar*	Salmonidae	Fishway
Briggs and Post (1997a)	Rainbow trout	*Oncorhynchus mykiss*	Salmonidae	Activity and energetics
Briggs and Post (1997b)	Rainbow trout	*Oncorhynchus mykiss*	Salmonidae	Activity and energetics
Brodeur *et al.* (2001)	Atlantic salmon	*Salmo salar*	Salmonidae	Environmental monitoring
Brown (1999)	Common carp	*Cyprinus carpio*	Cyprinidae	Activity and energetics
Brown (1999)	White sucker	*Catostomus commersoni*	Catostomidae	Activity and energetics
Brown (1999)	Brown trout	*Salmo trutta*	Salmonidae	Activity and energetics
Brown and Geist (2002)	Chinook salmon	*Oncorhynchus tshawytscha*	Salmonidae	Migration
Brown *et al.* (1999)	Rainbow trout	*Oncorhynchus mykiss*	Salmonidae	Activity and energetics
Brown *et al.* (2000)	Common carp	*Cyprinus carpio*	Cyprinidae	Activity and energetics
Brown *et al.* (2002)	Chinook salmon	*Oncorhynchus tshawytscha*	Salmonidae	Methodological
Brown *et al.* (2002)	Chinook salmon	*Oncorhynchus tshawytscha*	Salmonidae	Fishway
Bunt (1999b)	Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	Fishway
Chandroo *et al.* (in review)	Rainbow trout	*Oncorhynchus mykiss*	Salmonidae	Aquaculture
Chandroo (2000b)	Rainbow trout	*Oncorhynchus mykiss*	Salmonidae	Aquaculture
Chandroo (2000c)	Rainbow trout	*Oncorhynchus mykiss*	Salmonidae	Aquaculture
Cooke (unpublished data)	Blue catfish	*Ictalurus furcatus*	Ictaluridae	Activity and energetics
Cooke (unpublished data)	Channel catfish	*Ictalurus punctatus*	Ictaluridae	Activity and energetics
Cooke (unpublished data)	Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	Environmental monitoring
Cooke (1999)	Channel catfish	*Ictalurus punctatus*	Ictaluridae	Environmental monitoring
Cooke and Schreer (2003)	Common carp	*Cyprinus carpio*	Cyprinidae	Environmental monitoring
Cooke *et al.* (2000b)	Largemouth bass	*Micropterus salmoides*	Centrarchidae	Catch and release
Cooke *et al.* (2000c)	Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	Catch and release
Cooke *et al.* (2001a)	Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	Activity and energetics
Cooke *et al.* (2001a)	Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	Methodological
Cooke *et al.* (2001b)	Largemouth bass	*Micropterus salmoides*	Centrarchidae	Reproduction
Cooke *et al.* (2002b)	Largemouth bass	*Micropterus salmoides*	Centrarchidae	Reproduction
Cooke *et al.* (2002b)	Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	Reproduction
Cooke *et al.* (2002c)	Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	Catch and release
Demers *et al.* (1996)	Largemouth bass	*Micropterus salmoides*	Centrarchidae	Activity and energetics
Demers *et al.* (1996)	Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	Methodological
Demers *et al.* (1996)	Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	Activity and energetics
Einum (2002)	Atlantic salmon	*Salmo salar*	Salmonidae	Reproduction

Table 1 continued

Citation	Common name	Latin name	Family	Study application
Geist *et al.* (2000)	Chinook salmon	*Oncorhynchus tshawytscha*	Salmonidae	Methodological
Geist *et al.* (2002)	White sturgeon	*Acipenser transmontanus*	Acipenseridae	Methodological
Gowans (1998)	Atlantic salmon	*Salmo salar*	Salmonidae	Fishway
Healey *et al.* (2003)	Sockeye salmon	*Oncorhynchus nerka*	Salmonidae	Reproduction
Hennyey (1999)	Rainbow trout	*Oncorhynchus mykiss*	Salmonidae	Aquaculture
Hinch and Bratty (2000)	Sockeye salmon	*Oncorhynchus nerka*	Salmonidae	Fishway
Hinch and Rand (1999)	Sockeye salmon	*Oncorhynchus nerka*	Salmonidae	Methodological
Hinch and Rand (1999)	Sockeye salmon	*Oncorhynchus nerka*	Salmonidae	Migration
Hinch *et al.* (1996)	Sockeye salmon	*Oncorhynchus nerka*	Salmonidae	Methodological
Hinch *et al.* (1996)	Sockeye salmon	*Oncorhynchus nerka*	Salmonidae	Migration
Hinch *et al.* (2002)	Sockeye salmon	*Oncorhynchus nerka*	Salmonidae	Migration
Hinch *et al.* (2002)	Pink salmon	*Oncorhynchus gorbuscha*	Salmonidae	Migration
Kaseloo *et al.* (1996)	Lake trout	*Salvelinus namaycush*	Salmonidae	Reproduction
McKinley and Power (1992)	Lake sturgeon	*Acipenser fulvescens*	Acipenseridae	Methodological
McKinley and Power (1992)	Lake sturgeon	*Acipenser fulvescens*	Acipenseridae	Activity and energetics
Murchie (unpublished data)	Brook trout	*Salvelinus fontinalis*	Salmonidae	Activity and energetics
Murchie (unpublished data)	Walleye	*Stizostedion vitreum*	Percidae	Activity and energetics
Økland *et al.* (1996)	Atlantic salmon	*Salmo salar*	Salmonidae	Reproduction
Økland *et al.* (1997)	Atlantic salmon	*Salmo salar*	Salmonidae	Methodological
Økland *et al.* (2000)	Atlantic salmon	*Salmo salar*	Salmonidae	Reproduction
Schreer and Cooke (2002)	Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	Environmental monitoring
Smeddes (1997)	Rainbow trout	*Oncorhynchus mykiss*	Salmonidae	Catch and release
Standen *et al.* (2002)	Pink salmon	*Oncorhynchus gorbuscha*	Salmonidae	Migration
Standen *et al.* (2002)	Pink salmon	*Oncorhynchus gorbuscha*	Salmonidae	Methodological
Standen *et al.* (2002)	Sockeye salmon	*Oncorhynchus nerka*	Salmonidae	Migration
Thorstad *et al.* (2000)	Brown trout	*Salmo trutta*	Salmonidae	Methodological
Thorstad *et al.* (2000)	Lake trout	*Salvelinus namaycush*	Salmonidae	Methodological
Ueda *et al.* (2000)	Masu salmon	*Oncorhynchus masou*	Salmonidae	Activity and energetics
Weatherley *et al.* (1996)	Lake trout	*Salvelinus namaycush*	Salmonidae	Reproduction

Only those studies that utilized Lotek EMG transmitters are summarized. Studies were categorized relative to the study application.

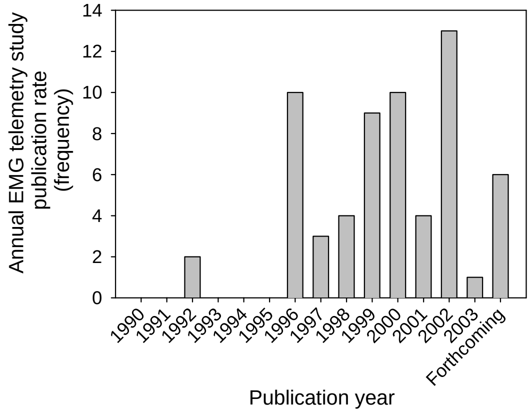

Figure 2 Trends in the annual publication rate of EMG telemetry studies between 1990 and February of 2003 ($N = 65$). Forthcoming papers include those that are in various stages of preparation or review, but are minimally at the draft stage. Additional studies that are 'forthcoming' may exist but were not located in our searches or queries of EMG researchers. The studies included in these analyses were limited to those that utilized the Lotek EMG transmitter.

activity. Some studies have removed a small amount of shielding from the end of the electrode wires and placed these directly into the axial musculature (5% of the studies, $N = 3$). To hold the electrode tips in place, the wires were bent slightly to create a hook by some authors. Ueda *et al.* (2000) also describes a technique where a small amount of exposed stainless steel electrode wire was placed in the musculature with no mention of a hook. This method is similar to that employed in electrophysiological studies (Jill Leonard, unpublished data) but can be prone to electrode shifting. Another method that has not been used frequently is the external securing of electrodes using plastic discs (Demers *et al.* 1996). The actual electrode for that technique was small amounts of unshielded wire. These different techniques have all been somewhat successful in obtaining reliable EMG signals, but the most common technique is to attach gold tips to the electrode wires (95%, $N = 58$).

McKinley and Power (1992) were the first to use the gold tips because of their inert characteristics. The gold electrodes were affixed to the end of the unshielded electrode wires. The wire was first passed through a hole that was drilled through the electrode and was then secured to the electrode by a combination of wrapping and twisting the wire. The gold bar created an L- or T-type junction that helped to anchor the electrode in the musculature. The Hinch lab (Scott Hinch, personal communication) switched from the L-type to the T-type after slippage was noted from Pacific salmonids recaptured in a moribund state. This approach has been widely adopted and is currently the most utilized method for securing the electrode in the musculature. The size of the gold electrode and the karat has varied among studies. The size of the electrodes is generally either 5 (20%, $N = 9$), 7 (60%, $N = 27$) or 10 mm (20%, $N = 9$) long with a diameter of ~1 mm. From experience, 7 mm size seems to be an easy length of electrode to place in the musculature and sufficiently long to anchor the electrode. Notwithstanding this general guideline, as EMG transmitter package size decreases and tags can be implanted in smaller individuals, it may be useful to investigate using smaller electrodes in smaller fish. Gold tips can be easily created by jewellers by cutting lengths of commercially available gold bars of the desired diameter into lengths, drilling holes for the wire and then smoothing rough edges. The type of gold has ranged from 9 to 24 karat, with most studies favouring 9 karat (55%, $N = 25$) because of cost and strength (14 karat: 22%, $N = 10$; 18 karat: 16%, $N = 7$; 24 karat: 7%, $N = 3$). The lower karat gold's higher levels of impurities strengthen the gold. It is currently unclear as to whether the karat of the gold affects signal detection or transmission. Some researchers have attempted to use hollow gold-plated electronic pins for electrodes (Charlene Lobsinger, personal communication). These pins are subject to rusting and have sharp edges and unknown signal transmission properties. For these reasons, we recommend that researchers use gold tips available from jewellers.

Electrode wires arrive from the manufacturer tightly wound. Based on our experience, we find that the transmitters function best if the wires are left wound as much as possible, without impeding the ability to place the electrodes. Several early studies (both field and laboratory) encountered problems with signal variability that were attributed to complete unwinding of the wires (Cooke, personal observation). The distance between the electrode wire, even when insulated, is proportional to the amount of background 'noise' and interference that they will collect (Larry Egan, personal communication). In addition, the electrode wires should be as short as possibly to minimize the distance to which the bioelectric signal must be transmitted. Longer wires may result in greater variability in electrode performance.

Surgical techniques

In general, most surgery times that encompass the period from when the fish becomes suitably anaesthetized (stage 5 anaesthesia; Ross and Ross 1999) until the last suture is completed range from 4 to 6 min (85% within this range, $N = 28$). Several of the early EMG telemetry studies that were developing techniques for the procedures used today were roughly double that time (~10 min; 15%, $N = 5$). Specific applications may also take longer time, such as those that involve fish shown to actively expel internally implanted transmitters such as the ictalurids. Additionally, reproductive-phase fish with highly developed gonads may also require longer surgical times to avoid damaging engorged reproductive organs. It is unlikely that the 4–6-min duration can be appreciably decreased as it usually takes just slightly longer to complete than the intraperitoneal implantation of conventional radio-transmitters.

Within a study, we recommend that the same surgeon conduct all the EMG surgeries because the standardization of the surgeon whenever possible will reduce possible unwanted variation in surgical outcome. Although not difficult, this technique does require more skill than basic transmitter implantation. Recent research on fish surgery suggests that more experienced surgeons have better surgical outcomes and more consistent surgical technique, and complete surgeries more rapidly than novices do (Cooke *et al.* 2003a). Individuals not familiar with this technique should first become proficient with basic surgical skills (suturing, scalpel work) prior to placing the electrodes. Electrode placement is one of the most important components of the EMG surgery. The electrodes must be placed parallel in the appropriate musculature in the appropriate location on the body, all of which require substantial practice. Additionally, when using the plungers to place the electrodes, care must be used not to damage viscera or prematurely eject the electrode.

In almost all the studies, the EMG transmitter package was implanted in the intraperitoneal cavity (98%, $N = 57$; see Fig. 1). This involves the construction of a small incision in the body wall usually in the ventral surface of the fish. When implanting upriver-migrating salmonids in preliminary studies, Hinch (unpublished data) discovered water hardening of eggs when fish were implanted intraperitoneally. To remedy this problem, the researchers created a small pocket between the musculature and integument by gently separating these tissues with their fingers into which the transmitter package was placed (Healey *et al.* 2003). The electrodes and electrode wires were run subdermally to the desired electrode placement site. This method of subdermal placement is effective for specific instances such as working with reproductively mature fish that are semelparous, but may not be suitable for small fish or for long-term monitoring. At present, subdermal placement of transmitters only comprise 2% of all studies ($N = 1$). To our knowledge, there are no examples of external attachment of EMG transmitters. Although theoretically possible for specific applications (e.g. when morphology prohibits internal implantation), external EMG transmitters would likely provide useable data for shorter periods of time. External transmitters would have a propensity to become fouled and increase drag, and may increase chances of electrode shift.

Electrode placement

Theoretically, EMG transmitters could be placed in a variety of muscles and muscle types in fish. Unlike conventional hard-wired electromyography where electrodes are placed in a single myomere, EMG telemetry electrodes generally span several myomeres. Although there have been no studies that have investigated the effects of implanting EMG telemetry electrodes in one or multiple myomeres, adjacent myomeres tend to respond closely in time and function to produce integrated swimming movement, suggesting that for EMG telemetry it not important to isolate individual myomeres. As most applications of EMG transmitters have been interested in locomotory activity, the electrodes have been placed in axial swimming musculature. A generalized example of axial musculature would include glycolytic white muscle that comprises the bulk of the swimming musculature and is used for anaerobic burst-type activity, a narrow outer band of red oxidative musculature for sustained aerobic swimming and some intermediate pink fibre types. As most studies are concerned with day-to-day activity, EMG electrodes are usually placed in the aerobic red musculature. Indeed, 97% ($N = 63$) of all EMG telemetry studies have attempted to place the electrodes in the red muscle (see Fig. 1). This band generally can be located under the lateral line. Although during burst exercise, the majority of muscle recruitment occurs in white muscle, there is some evidence that red muscle fibres are also recruited during this period (Burgetz *et al.* 1998). In addition, because of the strong electrical signal from the white muscle, this signal may also be picked up when the electrodes are in the red muscle. At present, it is unknown whether the amount of white muscle utilized is fully quantifiable as muscle potentials from more distant fibres are less likely to be detected. Thus, by implanting electrodes in red muscle, it is generally possible to assess activity during all modes of swimming that utilize axial myomeres. Early confirmational studies by Beddow and McKinley (1999) examined the placement of the EMG transmitter electrodes in different muscle types and also compared that output to raw EMGs obtained using an amplifier and digital strip recorder. They determined that regardless of longitudinal position in the body (0.5 and 0.7 body lengths), EMG activity from both transmitters and conventional hard-wire electromyography increased steadily with swimming speed in red muscle, whereas white muscle was only recruited at ~85% of critical swimming speed. The authors suggested that the majority of activity being recorded by the electrodes in red muscle of Atlantic salmon was aerobic, and that the signals were generally unaffected by white muscle activation during bursting. More recently, Brown *et al.* (2002) also calibrated chinook salmon using two EMG transmitters in the same fish, with one pair of electrodes in red muscle and one pair in white muscle. The authors used break point analysis to determine at what speeds fish transitioned from aerobic (red muscle) to anaerobic (white muscle) activity and used this to apply an anaerobic 'tax' on their field-collected data. These two studies (Beddow and McKinley 1999; Brown *et al.* 2002) represent the only studies where electrodes were placed in white muscle or both muscle types (3%, $N = 2$). Other researchers working on species with less red muscle or smaller species (e.g. centrarchid fishes) have found it difficult to entirely isolate electrodes in red muscle, which may lead to the recording of a combination of red and white muscle activity (e.g. Cooke *et al.* 2002b).

The location of the electrodes longitudinally along the body has also varied among studies. Unfortunately, the majority of studies (65%, $N = 42$) did not report the location of the electrode placement, or indicate if this was standardized among individuals. Of the remaining 23 studies that indicated location of electrode placement, several studies simply report morphological landmarks such as below the dorsal fin (26%, $N = 6$). Other studies provide quantitative reference, usually with regard to the proportional distance from the snout to the tail. Most studies (52%, $N = 12$) place the electrodes at ~0.7 body lengths from snout to tail (Fig. 1), with fewer studies (22%, $N = 5$) placing the electrodes at 0.5 body lengths from snout to tail. Beddow and McKinley (1999) compared EMG transmitter activity at 0.5 and 0.7 body lengths in Atlantic salmon and determined that EMG activity varied significantly among longitudinal positions along the fish. The authors suggested that EMG electrode placement should be standardized to 0.7 body lengths close to the tail region, while taking into account factors such as basic anatomy, swimming mode, aerobic capacity and relative fibre proportions.

There has been little effort to report the side of the fish into which electrodes were placed in the current body of EMG literature. Interestingly, Økland *et al.* (2000) noted that for fish with electrodes on the right side of the body, higher muscle activity signals were recorded when the fish contracted the right-side musculature during turning. They suggest that researchers may want to consider monitoring EMG signals from both sides of the fish simultaneously. To our knowledge, this has not been done by any researchers. We encourage researchers to standardize EMG electrode placement on the left side of the fish in accordance with fish sampling and enumeration procedures to minimize possible variation.

The gold-bar-type electrodes can be easily placed in the musculature using plunger-type devices. The first type of plunger is described in detail by McKinley and Power (1992) and is by far the most common (83%, $N = 44$). It consists of a hollow stainless steel rod (#20 gauge) with a groove for the gold tip. Smaller solid stainless steel rods sized to fit inside the hollow tube serve as a plunger. The stainless steel plunger tool ideally utilizes two separate plungers or one plunger used twice in sequence. Bunt (1999a) described a tool to facilitate the placement of paired electrodes at a standardized distance apart (distance can be changed); however, it has yet to become common place as evidenced by only one study that has used that technique (2%, $N = 1$). The two plungers are connected, and when depressed, the electrodes are simultaneously ejected into the musculature. The design described by Bunt (1999a) made use of laboratory consumables (e.g. syringes, needles) to construct the plunger. The limitation of this device is that it is larger than using long individual plungers, and this may require a larger incision. The device described by Bunt (1999a) used rather short needles that could be lengthened for larger fish. The flexibility afforded by individual rod-type plungers is greater than the device described by Bunt (1999a), so most researchers continue to use that method to place the electrodes. Chandroo (2000d) described a device similar to that of Bunt (1999a); however, Chandroo (2000d) used stainless steel spinal tap needles that provide additional length, and the larger amount of metal increases the sturdiness of the device. The Chandroo tool (Chandroo 2000d) has been used in a few studies (6%, $N = 3$). The remainder of the studies (9%, $N = 5$) used external anchors to secure the electrodes, as discussed under electrode designs.

The distance between electrodes has varied among studies (range 1–20 mm). Of the 47 studies that reported distance between electrodes, the majority (70%, $N = 33$) reported that 10 mm was the target distance. As a result of some slippage or electrode placement mishaps, the electrodes may end up closer or farther apart. Indeed, Thorstad *et al.* (2000) reported that although they targeted ~10 mm as the ideal distance between electrodes, the actual distance ranged from 1 to 17 mm. Whenever possible, we urge researchers to attempt to separate electrodes as close as possible to the 10-mm mark. In addition, we also suggest that postmortems should be conducted whenever possible to verify proper electrode placement. When the electrodes get so close that they touch each other, the EMG signal will be disturbed and useless. It seems that if the electrodes are implanted too close (<10 mm), they can move slightly in the muscle leading to possibility of contact during high activity (Eva Thorstad, personal observation).

There is much room for more detailed electromyographic studies similar to those presented by Beddow and McKinley (1999) that integrate hard-wired and telemetric techniques to better understand the function of EMG transmitters, and the importance of electrode placement longitudinally, transversely or relative to individual myomeres in different species of fish.

Generalized surgical procedure

To aid researchers initiating studies that involve EMG transmitters, we have provided a generalized surgical method based upon the most typical methods employed in EMG telemetry studies. Most aspects of this procedure could be somewhat modified as required to tailor the techniques to the project- and organism-specific context. The transmitter should be prepared ahead of surgery, with 9 karat gold, 7-mm electrodes attached to the wires. The wires should be twisted as much as possible without restricting the ability to place the electrodes in the desired location.

The fish should be individually anaesthetized using an appropriate induction anaesthetic and placed dorsal surface down on a surgical table. During surgery, water containing an appropriate maintenance anaesthetic should irrigate the gills. A 3-cm incision (room for transmitter cross-sectional dimension and room for manoeuvring electrode placement rods) should be made on the ventral surface, usually just posterior to either the pectoral or pelvic girdle. Electrodes are generally positioned ~10 mm apart, in the red axial musculature below the lateral line (Fig. 1), using $16\frac{1}{2}$ gauge rods. We recommend the use of the plunger described by McKinley and Power (1992). Electrode placement should be standardized at 0.7 body lengths (Beddow and McKinley 1999) on the left side of the fish. Fingers placed on the integument of the fish can be used to determine the location of the plungers and verify proper placement. Once in position, a plunger is used to secure the electrodes in the muscle, allowing the rods to be removed. The transmitter is then inserted through the incision and pushed anteriorly into the body cavity. A 16.5-g hypodermic needle is then pushed through the body cavity wall, and the antenna wire passes through to the outside. The incision can be closed using approximately four independent sutures. A schematic of the transmitter and electrode placement is presented in Fig. 1.

Transmitter implantation effects

The effects of surgical intraperitoneal transmitter implantation have been well studied, although there are several studies that have specifically investigated the effects of EMG transmitter surgery and transmitter presence. The only aspect of the surgery that differs from conventional radio transmitter implantation is the placement of the electrodes in the axial musculature, and the actual presence of the electrodes and electrode wires in the tissue or intraperitoneal cavity. Both studies that have explicitly examined the effects of EMG transmitter implantation used swimming performance challenges to compare EMG transmitter carrying fish with controls. McKinley and Power (1992) determined that the swimming performance of lake sturgeon was unaffected by EMG transmitter attachment when fish were swam 3 weeks following surgery. Similarly, Beddow and McKinley (1999) determined that the critical swimming speed of Atlantic salmon was similar between transmitter carrying fish and controls 48 hours following surgery. However, Gowans (1998) reported that EMG transmitter-implanted Atlantic salmon did not ascend a fish ladder with the same proportion as fish tagged with conventional radio transmitters. The author attributed the poor passage rate to fungal infections that lead to mortality. These findings coupled with general surgical theory highlight the need to minimize handling of fish to be implanted with transmitters.

Although not quantitative, other studies have noted that EMG transmitter-implanted fish have spawned following transmitter implantation (e.g. Healey *et al.* 2003) or successfully ascended fishways (e.g. Hinch and Bratty 2000). Particularly, when using transmitters that weigh less than ~2% of the body mass of the fish in air, the use of EMG transmitters can usually be accomplished with negligible effects on the behaviour, energetics or performance of the fish. However, depending upon the study, even slight transmitter effects may be important. Thus, when considering the use of EMG transmitters, researchers should also assess the objectives of the study.

It is important to note that changes in EMG signals can be expected over time. Beddow and McKinley (1998) monitored the EMG activity of Atlantic salmon at two different acclimation temperatures (8 and 18 °C) over a 4-month period. The relationship between EMG activity and swimming speed changed over time, but this was generally not observed until the third month. Less EMG activity was detected, particularly in the warm acclimated group, during the third and fourth month. The authors caution that care should be taken when extrapolating calibration data over long periods of time. It is likely that changes in muscle properties, especially in the regions adjacent to the electrodes that were encapsulated in connective tissue, may be responsible for the change in EMG signals over time.

Calibration and analysis

The time elapsed between the implantation of the EMG transmitter and commencement of the collection of data has varied substantially among studies (range of 1 hour to 30 days). At present, most studies (72%, $N = 28$) began collecting data within 1 or 2 days of implantation, fewer studies at more than 2 days (20%, $N = 8$), and even fewer within several hours (8%, $N = 3$). The factor that usually influences this time period is the biology of the fish and the study objectives. For example, laboratory-acclimated fish of hatchery origin could be held in tanks for extended periods of time whereas upriver migrating salmonids could generally only be held for very short durations without disrupting migration.

Currently, one of the biggest debates among EMG telemetry users is the need for individual calibrations for all transmitter-implanted fish. The relative importance of calibration varies extensively as a function of the study objectives, study logistics and life history of the fish species. For example, the degree of calibration required for qualitative definition of relative or semiquantitative activity are much less demanding than that for detailed estimation of swimming speed or energy expenditure. Although all EMG transmitters' output should be strongly correlated with swimming speed, these relationships differ among transmitters, species and individuals within a population (e.g. Økland *et al.* 1997; Thorstad *et al.* 2000). Calibration is usually achieved by recording EMG signals as fish swim at various of speeds under forced-swimming conditions (e.g. McKinley and Power 1992; Demers *et al.* 1996; Cooke *et al.* 2001a). Care should be taken when calibrating transmitters in respirometers as forced steady-state swimming may not represent the more complex and costly swimming behaviours exhibited by fish in the wild (Videler 1993). A growing body of literature has highlighted the need to develop swimming assessments that better reflect the plasticity of swimming behaviours observed in the wild (e.g. Plaut 2001). When calibrating EMG transmitters, it is important to realize these deficiencies that may introduce error into the calibration procedure. Researchers also need to be cognizant of error that can be introduced during calibration. For example, when developing relationships between EMG and tail beats, it is important to recognize that under nonsteady-state swimming typical of field conditions, low tail-beat frequencies can be associated with large variation in tail-beat amplitude (Webb 1986).

We acknowledge that in ideal situations, all fish implanted with EMG transmitters should be individually calibrated prior to release. However, this may not be feasible where fish are only a few weeks from death (e.g. homeward-migrating Pacific salmon), and the added time and stress of calibrations could reduce migration ability (Standen *et al.* 2002). Alternatively, some researchers (Brown 1999) actually released fish without performing calibrations and then recaptured individuals with pulsed DC electrofishing (not detrimental to EMG tags) to perform calibrations at the conclusion of the study. However, there are many practical considerations that preclude the calibration of all individuals. Geist *et al.* (2002) suggested that the main practical difficulties include the inability to transport respirometers and the difficulty in transporting live fish without exposing them to undue stress or pathogens. In addition to these difficulties, biotic factors associated with different species and different life-history stages make calibration challenging without negatively affecting the behaviour, physiology or even fitness of the fish.

In some studies, no calibrations are conducted and researchers simply rely on the transmitter to provide information on the relative activity of the fish. At present, 37% ($N = 19$) of the EMG studies have not conducted calibrations. For those that conducted calibrations (63%, $N = 33$), relationships were developed for individual fish (52%, $N = 17$), for other individuals in a parallel study (30%, $N = 10$) or for other individuals in an unrelated study (18%, $N = 6$). To test some of these concerns regarding the consistency in performance of EMG transmitters, Geist *et al.* (2002) implanted the same transmitter into different groups of white sturgeon. The authors concluded that the same EMG transmitters usually did not produce the same results in different fish. When signals from different fish were grouped, the relationship used to predict swim speed from EMG signals was less accurate than if individual relationships were utilized. It was unclear from their results whether the differences in EMG transmitter performance reflected variation in individual locomotor performance or variation in placement and function of the EMG transmitters. Although the study by Geist *et al.* (2002) suggests that caution should be used when applying calibrations from one group of fish to another, the information provided by EMG telemetry is, in many cases, unattainable using any other method.

Of the studies that conducted calibrations, all studies ($N = 33$) relied upon relationships between EMG signals and swimming speed, whereas fewer studies collected information on the relationship between EMG and both oxygen consumption (33%, $N = 11$) and tail beats (30%, $N = 10$). The relationships between EMG signals and swimming speed are generally linear or log-linear (82%, $N = 22$), with R^2-values ranging from 0.10 to 0.99. Although not possible to determine precisely why swimming speed explains such a wide range of EMG variation, it likely reflects differences in fish species, body form, swimming mode and problems with the physical placement or choice of electrodes. Some researchers have found the relationships between EMG and swimming speed to be polynomial (18%, $N = 5$).

There are several approaches for standardizing data for use in drawing comparisons among different groups of fish or different individuals. Some methods of transformation require knowledge of the baseline EMG activity that corresponds with zero swimming speed. EMG resting levels differ among individual fish (e.g. Økland *et al.* 1997; Thorstad *et al.* 2000). This is probably partly caused by individual differences in electrode placement and muscle physiology, but the resting level also seems to differ among EMG transmitters, for unknown reasons. As indicated earlier, this may have to do with different individual variation in electronic component function. A correction of the data for individual differences in resting levels (see below) will reduce irrelevant variation in the data set and make comparisons easier. These resting EMG activity levels can be obtained in a number of different ways. Of the 30 studies (46%) that collected information on resting activity levels for standardizing data, 77% ($N = 23$) obtained resting values when fish were still prior to release, 13% ($N = 4$) when fish were still after release, and 10% ($N = 3$) collected resting values from anaesthetized fish. Visual observations when fish are held in tanks or respirometers during periods when they are stationary are the easiest method. When fish have been released into more expansive environments, divers can make detailed notes on fish activity correlated with EMG activity or data may be collected using videography for later transcription. Resting levels can also be obtained by examination of individual pulse intervals. EMG transmitters will provide some rather stable wide (maximal) pulse interval that indicates inactivity. By plotting up large strings of individual pulse intervals, data can be visually inspected for stable resting values. This method of obtaining resting EMG values that correspond to zero activity is extremely useful for scenarios when it is not possible to calibrate individual fish. Caution must be taken for the visualization approach in that some fish may always exhibit some low level of swimming activity that could be construed as 'resting'. These assessments are best supported by an independent measure of activity or only used for species or environments where genuine resting levels can be expected.

EMG telemetry data can be expressed in a variety of formats. The raw output from the EMG transmitter (pulse intervals) is inversely correlated with activity

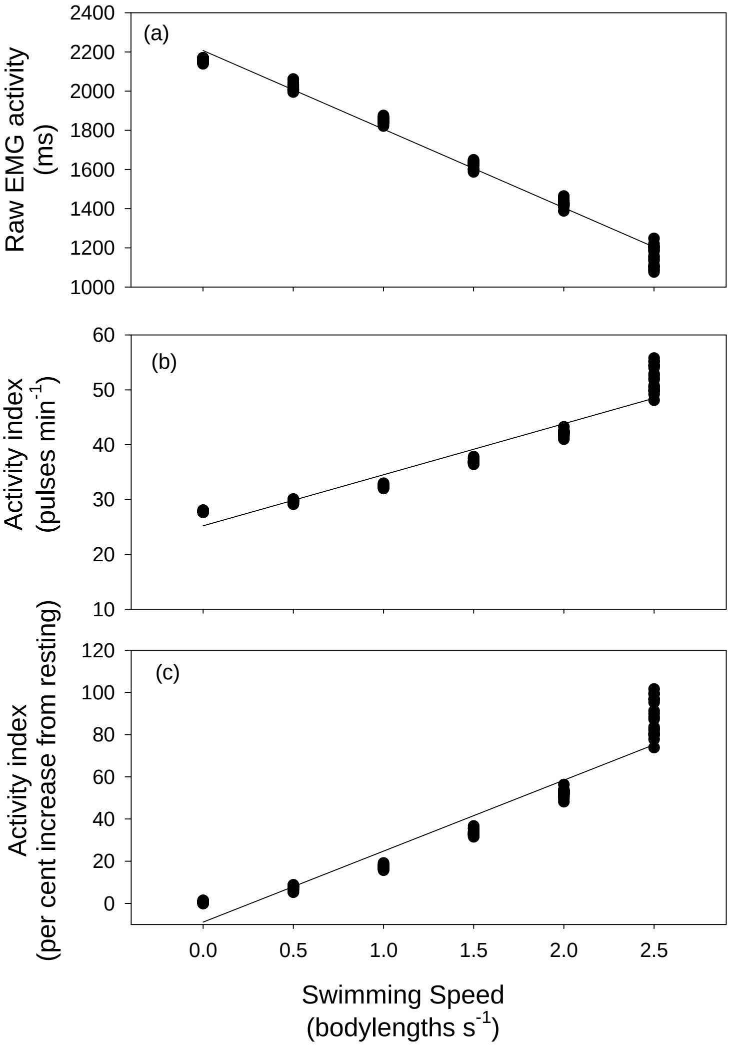

Figure 3 Visualization of data for a largemouth bass (TL = 302 mm, WT = 404 g) swam in a respirometer to illustrate the different methods of reporting EMG data ($N = 20$ data points per swim speed). Data are presented in (a) raw form, (b) as an activity index (p.p.m.) and (c) as an increasing activity index (% increase from resting). Linear regressions have been fitted to the data.

(Fig. 3a). This raw information has been used for analyses and visualization in 32% ($N = 19$) of the studies. The inverse relationship can be counterintuitive to non-EMG users, resulting in confusion. Other researchers have expressed EMG activity as either pulses per minute (17%, $N = 10$; Fig. 3b), or created an activity index that reports relative EMG activity as an increase above resting (Fig. 3c) or by dividing EMG pulse intervals during activity by the EMG average obtained at resting speed in individual fish (37%, $N = 22$). An activity index reporting EMG activity as an increase above resting has been used for the assessment of parental care providing bass (Cooke *et al.* 2002b), a situation when removal of the parental male from the nest for extended periods combined with exhaustive exercise in a swim tube would likely have resulted in abandonment and/or reduced reproductive success. For studies in which calibrations permit the determination of swim speeds, tail beats or some energetic equivalents, the data analysed and reported in the literature are usually based upon these values (e.g. swimming speed (cm s^{-1}), proportion of critical swimming speed, energy use (J hour^{-1})), instead of EMG output (15%, $N = 9$). Unfortunately, these more informative and biologically relevant data are only available when calibrations exist.

There have been few attempts to develop statistical approaches to deal with the large auto-correlated time series that are obtained using EMG transmitters. Indeed, a recent chapter on the analysis of telemetry data did not include any discussions of physiological telemetry data (Rogers and White 2003). One of the most common analysis techniques for EMG data is the use of repeated-measures analysis of variance models (see Hinch *et al.* 1996; Standen *et al.* 2002, for example) where 'individual fish' is the repeated variable – an important consideration for analysis because there can be significant differences in tag behaviour or implantation among subjects.

EMG telemetry applications

Project characteristics

Although the number of species in which EMG transmitters have been applied is steadily increasing (currently in 18 species), the majority of studies have focused on economically and recreationally important fish families such as salmonids and centrarchids (Fig. 4). Several researchers have also utilized EMG transmitters in nongame species such as white sucker and carp. The species limitations likely reflect to some degree the costs of this technology and the relative 'ease' with which it is possible to obtain funding for fishes with commercial or recreational value. The increasing body of literature on several groups of fishes does have some advantages. For example, developing calibrations for a suite of closely related species provide researchers with valuable data and may reduce the cost of future studies. Furthermore, numerous studies on a few species will eventually yield a large data set that could incorporate the seasonal, life-history and gender-specific components to develop and refine life-time energetics models. When investigating a new species that differs from the others, one must work from 'scratch' to develop calibrations and refine techniques. Population-level differences in muscle and swimming performance, and hence EMG transmitter performance may also exist (Økland *et al.* 1997). Many studies conducted to date have not included information on the gender of the fish (60%, $N = 39$), except those that focus upon reproductive ecology or migration energetics (40%, $N = 26$). Whenever possible, determination of gender could be used as another variable or standardized to eliminate this source of variation. At present, there are no studies that utilize Lotek's EMG transmitter that have occurred in marine environments.

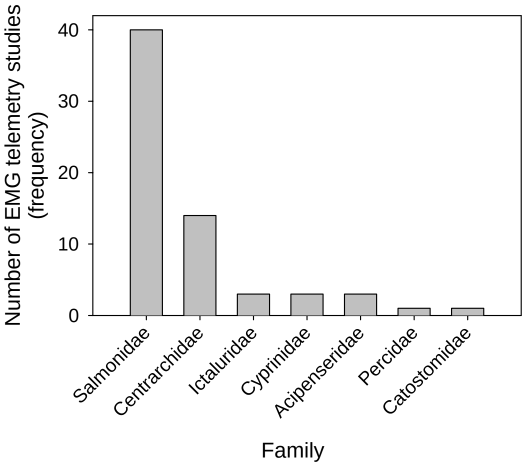

Figure 4 Family-level categorization of EMG telemetry studies in freshwater fish ($N = 65$). The studies included in these analyses were limited to those that utilized the Lotek EMG transmitter.

To date, most of the EMG telemetry studies have focused on either laboratory or outdoor experimental units such as research ponds or enclosures (e.g. Chandroo *et al.* 1999; Cooke 1999; Fig. 5). There has been a general reluctance to use transmitters in wild, free-ranging fish because of the inability to recover the fish or transmitter, potential widespread movement that could occur and the resulting difficulties in recording EMG signals. There has, however, been a few studies that have liberated relatively large numbers of fish in rivers to study the upriver migration of fishes (e.g. Hinch *et al.* 1996; Brown *et al.* 2002).

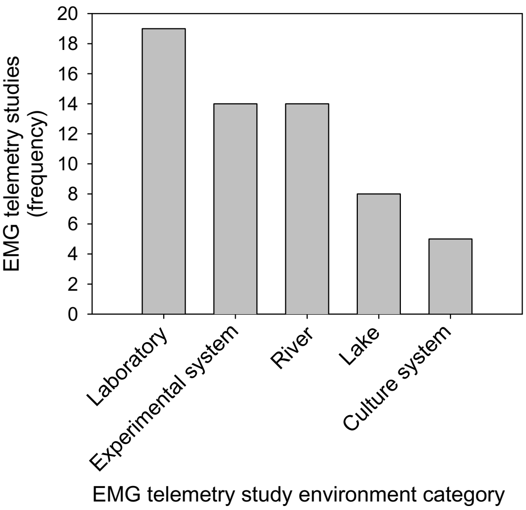

Figure 5 Environmental categorization of EMG telemetry studies of freshwater fish ($N = 65$). For those studies that were conducted in multiple environments, the location where research was focused was chosen as the site. Experimental systems included experimental spawning channels, experimental ponds, and experimental raceways. Culture systems included those studies that were explicitly conducted in an aquaculture setting. The studies included in these analyses were limited to those that utilized the Lotek EMG transmitter.

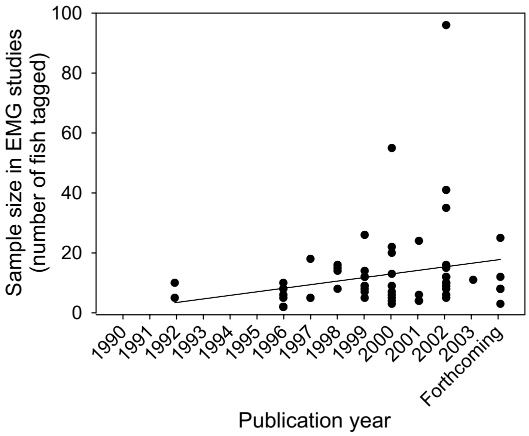

Figure 6 Trends in sample sizes (number of fish tagged) of EMG telemetry studies in freshwater fish between 1990 and February of 2003 ($N = 65$). Forthcoming papers include those that are in various stages of preparation or review, but are minimally at the draft stage. The studies included in these analyses were limited to those that utilized the Lotek EMG transmitter.

As with any type of study, sample size is an important consideration for studies employing EMG transmitters. However, EMG transmitters are costly. For example, it may be better to obtain more complete and detailed records on several individuals than disparate and incomplete data on numerous individuals. These issues are particularly important when considering studies in which fish are mobile or diffuse, making the simultaneous monitoring of numerous individuals challenging. Indeed, Brown (1999) deployed fewer EMG transmitters in a second field season to obtain more complete data sets on those individuals. In some cases, substantial information can be gained from one or two individuals to supplement other data. However, if statistical approaches are to be applied, then larger sample sizes are required. Sample sizes have been increasing over time as the validity of the technique and value of the data are illustrated. Several recent studies funded by large-power utilities have released as many as 91 EMG transmitter-implanted fish in a single study (e.g. Brown *et al.* 2002). We cannot provide a standard sample size as the objectives and logistical constraints vary widely among studies, but we are encouraged by the trend in increasing sample sizes observed in the studies that we reviewed (Fig. 6).

Applications

Many of the first papers published on EMG telemetry were methodological, but EMG transmitters are increasingly being applied in fields such as aquaculture, reproductive ecology and physiological energetics (Fig. 7). Research utilizing EMG transmitters was classified into eight general categories including methodological research. Given below are seven general categories of EMG applications identified from

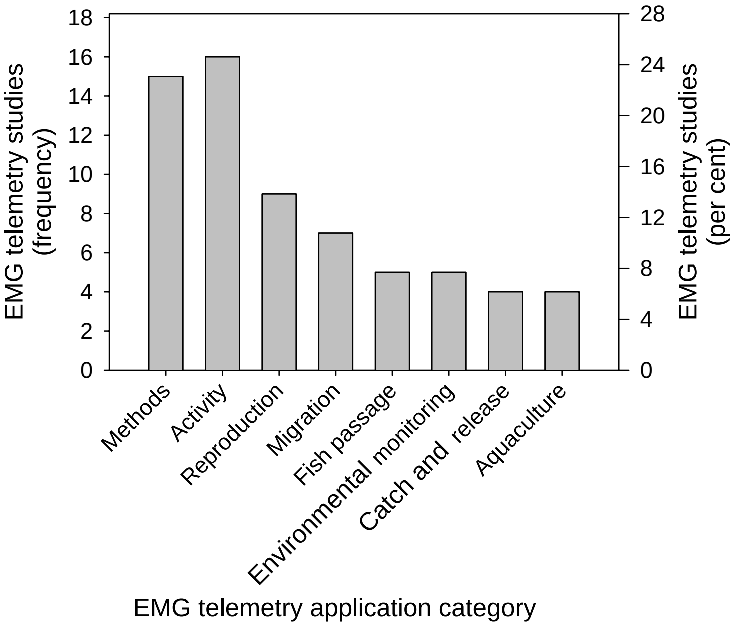

Figure 7 Application categorization of EMG telemetry studies in freshwater fish ($N = 65$). Methods studies were those that were devoted specifically to calibration or validation of EMG transmitter function. The activity category also included all energetics studies. Reproduction excluded those studies associated with upstream migrations, and the migration category excluded all those studies associated with fish passage. The studies included in these analyses were limited to those that utilized the Lotek EMG transmitter.

the review to provide brief overviews of the advances that have been made owing to the application of EMG transmitters. Methodological studies were excluded as information regarding calibrations, and other technical details were discussed above.

Activity and energetics

The most studies conducted using EMG telemetry have focused on activity and energetics (Fig. 7). EMG telemetry can clearly provide information on movement and activity at a resolution that is not possible using conventional telemetry. The first evidence supporting this idea was presented by Lucas *et al.* (1991). The authors determined that while using heart rate transmitters, EMG interference signals recorded incidentally indicated local activity that could not be detected by mobile tracking. Using EMG telemetry, Demers *et al.* (1996) also recognized that fish may exhibit periods of localized activity that are undetectable using conventional telemetry. In their study of smallmouth bass and largemouth bass in a small lake, they found that activity patterns determined by EMG telemetry activity were quite variable, although this activity was not evident when simply triangulating the location of individual signals. Building on that work, Cooke *et al.* (2001a) compared the activity and movement rates of smallmouth bass in a Lake Erie mesocosm using EMG telemetry, a fixed antenna array with coded radio transmitters, and an angling mark-recapture study with external anchor tags. The activity levels for fish in the mesocosm varied substantially with the technique that was employed. Smallmouth bass monitored with EMG telemetry were estimated to move the most (an equivalent of 27 km day^{-1}), those monitored with anchor tags moved the least (~50 m day^{-1}), and those monitored with conventional fixed telemetry moved intermediate distances (~80 m day^{-1}). Indeed, as activity often occurs over finite temporal and spatial scales, EMG telemetry is particularly well suited for assessments of activity and energetics.

Briggs and Post (1997a,b) conducted some of the first and most detailed assessments of the field activity and energetics of free-swimming fish. Using careful calibrations, the authors determined seasonal energy budgets for rainbow trout in a small pond at temperatures ranging from 3 to 22 °C. The authors determined that activity metabolism was less than half that of standard metabolic rate (Briggs and Post 1997a,b). In addition, activity metabolism was generally crepuscular, with minimal values observed prior to dawn (Briggs 1995).

Several studies have focused on examining the winter ecology of fish, a chronically understudied period of fish life history. Brown *et al.* (1999) examined the swimming activity of rainbow trout in an experimental flume during exposure to supercooling, frazil ice and anchor ice. EMG activity revealed that during exposure to frazil and anchor ice, fish activity was either stable or depressed relative to non-ice conditions. The duration of exposure to supercooled water was negatively correlated with the activity level of the fish. During supercooling, the escape response of EMG transmitter fish were also muted. In field conditions, Brown (1999) quantified the swimming activity and diel activity patterns of brown trout, white sucker and common carp in the Grand River, Ontario, during the winter. None of the species studied displayed conspicuous daily winter activity rhythms. All the species studied were active during winter periods. Activity patterns and swimming activity were influenced by water temperature, flow and ice conditions. White sucker and brown trout swam an equivalent of ~15–18 km day^{-1}. Common carp were significantly more active, with two fish swimming an equivalent of 25 and 40 km day^{-1}. Interestingly, Brown (1999) determined that during the winter, fish have varying energetic demands that are influenced by environmental factors in a similar manner to other seasons. An important finding of this work was that fish may respond to changing ice conditions with energetically costly activity levels. For example, Brown *et al.* (2000) determined that common carp responded to the formation of a hanging dam (thick subsurface accumulation of frazil ice) with variable individual activity patterns.

One of the first studies of EMG telemetry examined the activity and energetics of lake sturgeon (McKinley and Power 1992) downstream from a hydro-generation facility. The authors determined that sturgeon were more active during the summer than during the winter (note that their published interpretation is inverse because of a mix-up with the pulse intervals; see Figure 4 in McKinley and Power 1992), and that diel activity patterns were generally undetectable. At times, fish exhibited bursting activity that corresponded to ~50% of their scope for activity. Although their research occurred downstream from a hydro-generation facility, the authors did not present any information on how fish responded to changing flows. More recently, the question of how fish respond to fluctuating discharges associated with hydro-generation facility has been examined using EMG telemetry. A forthcoming study on brook trout and walleye in northern Ontario determined that EMG telemetry was an effective tool for monitoring fine-scale patterns associated with altered flow regimes (Karen Murchie, unpublished data). Responses to altering flow conditions were readily detectable from EMG activity patterns, which will eventually permit ascribing costs to different flow conditions and the changes in flow.

Collectively, the data obtained using EMG telemetry suggests that fish activity occurs at a variety of temporal and spatial scales, and that fish can expend a substantial amount of their activity budget undertaking localized movements. For this reason, some of the most detailed field activity budgets for fish have been constructed using EMG telemetry (e.g. Briggs and Post 1997a,b; Brown 1999).

Reproductive ecology

Reproductive ecology in the context of this paper will focus on actual courting, spawning and/or parental care periods, and will exclude migrations that are discussed separately below. There have been several studies that have used EMG telemetry to assess the physical activity and energetic costs of the actual spawning act. The first study involved assessing the ability of EMG transmitters to indicate reproductive activity in lake trout in a laboratory spawning raceway (Kaseloo *et al.* 1996). Peak EMG activity was associated with alignment and gamete deposition during spawning at dusk. The authors concluded that EMG records could serve as an indicator of spawning activity in lake trout. Next, the same research group (Weatherley *et al.* 1996) evaluated lake trout spawning in an experimental lake in central Ontario. They used EMG transmitters to assess muscular activity indicative of spawning behaviour during periods when fish were spawning in deep water and at night when spawning cannot be visually observed.

In a preliminary study, Økland *et al.* (1996) examined the reproductive activity of Atlantic salmon in a spawning tank. The authors concluded that EMG transmitters were able to document varied activity levels associated with different behaviours. More recently, the same research group attempted to quantify physical activity associated with specific spawning behaviours of Atlantic salmon in a seminatural river in Norway (Økland *et al.* 2000). In that study, the authors determined that breeding-related behaviours such as display, quivering and spawning by males and probing, digging and spawning by females corresponded well with EMG signals. The authors also determined the relationship between EMGs and swimming speeds in free-swimming fish. This made it possible to translate the activity level during different breeding-related behaviours to corresponding swimming speeds. A similar study by the same research group compared the muscular activity during reproduction in wild, sea-ranched and farmed Atlantic salmon (Einum 2002). The authors concluded that across all stocks, the energetic costs associated with reproductive behaviour are larger in male than in female Atlantic salmon. In addition, using data from EMG transmitters, they concluded that reductions of reproductive success in cultured salmon do not appear to be related to differences in their energetic investment in reproductive behaviour. Healey *et al.* (2003) estimated the energy expenditure during reproduction of sockeye salmon in British Columbia using EMG telemetry. EMG data when combined with detailed visual observations provided behaviour-specific costs for a variety of reproductive activities including holding prior to spawn, courting and spawning. The entire energy budget for the reproductive period constructed using EMG telemetry data corresponded with previous studies utilizing destructive proximate body composition analyses, while providing detailed information on the relative costs of different behaviours.

In addition to the research on salmonids outlined above, research on reproductive activity has also focused on the centrarchid black bass. Cooke *et al.* (2001b) examined the physical activity and behaviour associated with spawning of largemouth bass in ponds in Illinois. The researchers identified periods during the spawning event when physical activity was highly correlated for male and female bass. The authors also identified several breeding-related behaviours (i.e. shuddering, courting and aggression) that resulted in elevated locomotory activity. Similar to work on lake trout (i.e. Weatherley *et al.* 1996), it was suggested that occurrence, timing and duration of spawning-related behaviours can be inferred from EMG activity (Cooke *et al.* 2001b). In another study, Cooke *et al.* (2002b) compared the energetics of male parental care in largemouth bass and smallmouth bass in an eastern Ontario lake. Both species of bass were active diurnally and exhibited patterns of activity that differed among stages of offspring development. Both species swam large distances in very localized areas, in some cases covering more than 50 km day^{-1}. Interestingly, largemouth bass did not exhibit the pattern of investment that would be expected based upon the trade-offs between current and future reproduction. Using the data on activity across the parental-care period, the authors estimated the energetic cost of parental care for both largemouth bass and smallmouth bass using swimming speeds and the Wisconsin Bioenergetics model (UW Sea Grant 1997). The study by Cooke *et al.* (2002b) suggested that EMG telemetry provided insights into the behaviour and physiological energetics of the parental care period that would facilitate the development of seasonal, gender-specific energetics models (Ney 1993). Future assessments that incorporate costs associated with the use of paired fins (i.e. pectoral fins) assessed with EMG transmitters would further improve these energetics models.

For all studies of reproductive ecology incorporating EMG telemetry, researchers supplemented EMG data with detailed observations on individual behaviour derived from time-stamped videography or audio recordings of EMG signals that correspond to visual observations collected in the laboratory or field. For studies in which one of the objectives was to simply identify spawning, authors recommend some form of confirmatory measurements (e.g. egg baskets, gonado-somatic index scores) to support the data provided by EMG telemetry (e.g. Weatherley *et al.* 1996). Healey *et al.* (2003) also used conventional locational telemetry as a means to supplement data on the duration of behaviours in individual fish obtained from EMG transmitters. Additional laboratory research on the costs of nonswimming EMG activity would be useful to assess the validity of equating EMG values to swimming speed costs for nonswimming behaviours (e.g. shuddering, digging).

Migration

An extensive assessment of upstream migration of Pacific salmon initiated in the early 1990s in the Fraser River watershed, British Columbia, has used EMG telemetry as a central research tool. In their first published study on this topic, Hinch *et al.* (1996) examined the upstream migration of sockeye salmon through several reaches of the Fraser Canyon. The authors determined two locations where fish experienced difficulty and expended much energy. One of these locations had not previously been regarded as a region where sockeye salmon experience migration difficulty. In addition, three other regions that were historically viewed as areas of difficulty were actually determined to be relatively easy for sockeye salmon to pass. Building on these studies, Hinch and Rand (1998) evaluated swimming speeds and energy use of upriver-migrating sockeye salmon associated with local environment and fish characteristics. Gender was determined to be an important factor, with highest efficiency for females. The authors also identified differences in migration behaviour and costs associated with body size within male fish, and among years for male fish. The river characteristics associated with inefficient swimming patterns and energy use were those with constrictions in flow, which tended to generate turbulence and thus perhaps confusing migrational cues.

Using the data collected in previous EMG telemetry studies, Rand and Hinch (1998) modelled the risk of energy depletion associated with different environmental factors experienced by the fish and the biotic condition of the fishes. Using Monte Carlo hindcasting simulations from 1950 to 1994, the authors predicted that 8% of the salmon runs during that period would have resulted in a high mortality risk to the average migrant. The model developed by these researchers can be used by management agencies to help make fisheries decisions with risk-averse strategies. Interestingly, the authors determined that a 5-s data collection time scale was required to effectively predict the energetic costs of migration. Averaging activity over longer time periods (hours, days) failed to incorporate the full costs of anaerobic bursting activity, emphasizing the need for the high-resolution data provided by EMG transmitters. Smoothing of EMG telemetry data by averaging over time scales as small as 1 min may result in significant underestimates of the true costs of activity. We encourage the development of analysis techniques that recognize the importance of short-duration/high-intensity muscle activity into energetics models.

Some of the most recent work by this research group focused on the comparative swimming patterns and behaviour of upriver-migrating pink and sockeye salmon (Hinch *et al.* 2002). Although average swimming speeds were similar among species, sockeye salmon speeds were more than twice as variable as those of pink salmon. Despite differences in variability, there was no difference in the proportion of time that fish of each species spent engaged in three different types of swimming (burst, prolonged and sustained). In a companion study, the same authors (Standen *et al.* 2002) estimated the costs of migration through the Fraser Canyon for the same two species. The authors were unable to resolve any differences in the energetic cost of migration for pink and sockeye salmon. Instead, reach characteristics associated with degree of constriction tended to increase costs for both species.

A second research group also working in a large river system in the Pacific north-west has investigated the upstream migration of salmonids (Geist *et al.* 1997; Brown and Geist 2002; Brown *et al.* 2002). To date, their work has focused on chinook salmon in the Columbia River watershed. Their first study examined the energy expenditure of fall-migrating fish (Geist *et al.* 2000). Using data from a parallel EMG transmitter calibration study (both swimming speed and oxygen consumption), and known migration timing and distance for chinook salmon in the wild, the authors estimated energy expenditure of fish in the field. The authors concluded that data from EMG laboratory calibrations, when combined with field observations from telemetered fish, can provide a useful tool for modelling upstream migration costs.

To remedy the deficiencies in that modelling exercise (i.e. not actually measuring the EMG activity of fish in the wild), their research programme shifted to directly estimating energy expenditure and swimming speeds of EMG transmitter-implanted chinook salmon in the Klickitat River (Brown *et al.* 2002). In that study, fish had to negotiate three waterfalls and exceeded their critical swimming speeds more frequently during these attempts than when swimming between barriers. However, overall, fish spent more energy swimming between barriers than when attempting to ascend the waterfalls. Swimming speeds were highest during diurnal periods. The authors also modelled the effects of delayed passage in the lower reaches of the river on energy reserves that would be required to successfully reach the spawning grounds and reproduce. Additional work by this group focusing on fishway use is discussed under the fishway section of this synthesis (see Brown *et al.* 2002).

Researchers beyond North America have also been using EMG telemetry to examine migration energetics. Ueda *et al.* (2000) used EMG telemetry in a study of homing migration in masu salmon in Lake Toya, Japan. Prior to ascending streams to spawn, salmon in the lake exhibited very consistent swimming speeds. When fish ascended the streams, activity levels became quite variable. Some individuals migrated upstream early and spent extended periods in deep, quiet pools where they exhibited low activity levels.

Collectively, the studies outlined here have provided valuable information on the upriver migration of Pacific salmon. The models and refinement in model input parameters derived from EMG telemetry are aiding managers in making decisions regarding harvest allocations while minimizing risk to the stocks. In addition, these data could also be used to determine optimal water discharge regimes in regulated rivers during periods of migration and to aid in design of habitat modifications that affect flow (e.g. bank configurations, gravel bar management).

Fishway passage

Fishways are structures designed to facilitate the upstream passage of fish beyond a physical barrier such as a lowhead dam or a region of extremely high flow. Recent studies on fishways have focused on quantifying the difficulty and costs associated with use of these devices, and EMG transmitters provide a valuable tool for addressing these questions. The first study of fishway use was conducted by Booth *et al.* (1995, 1997) in an experimental fishway in Newfoundland. The authors detected two distinct patterns of swimming behaviour during ascent that were temperature dependent. At lower temperatures, swimming activity was characterized by a rapid increase in muscle activity that remained elevated throughout the ascent, whereas at higher temperatures, swimming was continuous and typically involved a constant increase in muscle activity throughout the ascent.

In Scotland, Gowans (1998) used EMG telemetry to assess the levels of physical activity associated with Atlantic salmon during ascent of the Conon Falls fish ladder. The author concluded that even under reasonably warm water temperatures, anaerobic burst swimming was required to ascend the fishway. The cost of fishway use can be substantial, especially when fish spend protracted periods within the fishway. In addition, the author observed substantial individual variation in EMG activity that may reflect different ascent strategies. In a similar study, Bunt (1999b) used EMG telemetry to compare the relative difficulty associated with smallmouth bass ascent of two differently configured fishways (slope, length and velocity) in south-western Ontario. EMG signals were significantly elevated in the upper reaches of both fishways relative to the entrance region. EMG telemetry revealed that fish used combinations of burst and prolonged swimming activity and that these values exceeded those generated through controlled swimming performance trials in laboratory swim tubes. The shorter but steeper fishway with higher water velocities required that fish elevated EMG levels beyond the levels recorded in the longer, less steep fishway with lower velocities.

In a study of upstream migration of sockeye salmon at a constriction with a fishway (Hinch and Bratty 2000), researchers determined that fish that did not successfully ascend the fishway exhibited one or more periods where they swam for 10 min or more at speeds greater than critical swimming speed. This was the first study to report that wild swimming salmonids were capable of instantaneous speeds in excess of 10 body lengths per second, levels that far exceed fish studied in laboratory environments. Successful fishway passage was characterized by steady and continuous swimming at relatively slow speeds that only exceeded critical speeds for less than 3 min. The authors concluded that hyperactivity was correlated with unsuccessful passage. Because of the large degree of individual variation, the authors also concluded that different individuals likely chose different migration paths and were faced with different environmental conditions (i.e. velocities, turbulence). In a similar study in the Columbia River, Brown *et al.* (2002) examined the energetic costs associated with passage of tailraces, fishways and forebays at the Boneville Dam by chinook salmon. Energy use was highest in the tailraces, intermediate while ascending fishways and lowest in the forebay. The authors also identified specific fishways in the complex that were more difficult and energetically costlier than others.

Collectively, studies on fishway use have provided fishway designers with information on how fish ascend fishways and where fish encounter difficulties. In one case, these data have been used to modify existing fishways in order to improve attraction and passage efficiency. Bunt (2001) reports on alterations made to a fishway after detailed assessments including EMG passage studies on smallmouth bass (Bunt 1999b; see discussion above) identified problem areas within the fishway.

Environmental monitoring and assessment

Electromyogram telemetry has been used to assess fish responses to a variety of pollutants ranging from chemical through physical. The physical stressor that has been best studied is thermal pollution. A comprehensive assessment of smallmouth bass responses to variable thermal conditions in a coal-fired effluent included EMG telemetry. Smallmouth bass that were free-swimming in the thermal effluent exhibited no distinct diel activity patterns (Cooke, unpublished data). Similarly, when smallmouth bass were held in cages in the effluent, activity was generally stable, but depressed relative to fish held in cages in Lake Erie (Schreer and Cooke 2002). The researchers also examined parental care activity of smallmouth bass in the thermal effluent and determined that fish exhibited patterns of parental-care investment that were not consistent with parental care theory or empirical assessments of smallmouth bass parental care activity (Cooke *et al.* 2003b).

In addition to this research on smallmouth bass, researchers working in the same thermal effluent also studied channel catfish (Cooke 1999) and common carp (Cooke and Schreer 2003) by using EMG telemetry in the winter. The channel catfish remained in deep water and spent little time in the canal, so detailed analyses were not possible, but a moderate correlation between mean daily water temperature and mean daily activity was observed (Cooke 1999; Cooke *et al.* 2000c). Carp were observed when free-ranging and when restricted to an enclosure (Cooke and Schreer 2003). The researchers determined that carp activity was variable, but fish were generally more active during periods of thermal change, and least active when water temperatures were stable.

EMG telemetry has also been used to evaluate the response of fish to chemical stressors. In fact, one of the earliest studies using EMG telemetry aimed to evaluate the response of rainbow trout to waterborne zinc (Weatherley *et al.* 1980). However, the publication arising from that study did not actually present any data on how fish responded to the contaminant. More recently, Brodeur *et al.* (2001) used EMG transmitters to evaluate the bioenergetic consequences of aluminium and acidic water on adult Atlantic salmon. Fish exposed to chronic elevated aluminium and acidic water exhibited increased activity levels related to control fish throughout the entire 20-day exposure period.

One of the problems with conventional assessments of pollutants in laboratory environments is the difficulty in replicating the synergistic effects and site-specific conditions present when fish face pollutants in the wild. Whole-animal assessments such as swimming activity could thus serve as sensitive indicators of changes in general organismal health (Beitinger and McCauley 1990). The field of aquatic pollution assessment and environmental monitoring could benefit immensely from increased incorporation of EMG telemetry (Cooke and Schreer 2003). These assessments could also facilitate determination of the bioenergetic consequences (Beyers *et al.* 1999) of exposure to different pollutants, an ecologically relevant approach that is becoming increasingly common. As activity is a major component of the bioenergetics model, EMG telemetry could provide necessary data in support of these projects.

Aquaculture

For some time, researchers have identified the benefits that could be derived from using telemetry in aquaculture. Despite several comprehensive reviews on the topic, only recently has telemetry become an important tool in aquaculture. The first EMG telemetry study in the field of aquaculture was an examination of the energetic costs and activity patterns of rainbow trout exposed to three different densities of culture (Cooke *et al.* 2000a). The authors determined that activity levels and resultant oxygen consumption levels increased from low to high densities. In addition, fish were more active during nocturnal and crepuscular periods.

A series of papers included by Chandroo (2000d) and Chandroo *et al.* (1999) examined other applied issues in aquaculture including the effects of different lighting regimens (i.e. on/off versus phased) and the effects of hauling on the activity of fish. Chandroo (2000c) determined that light shock associated with instant-on lighting systems caused fish to elicit fast-start responses indicative of escape or avoidance behaviour. In a follow-up study, Chandroo (2000b) exposed fish to both instant-on and natural-phased lighting regimens. EMG telemetry data suggest that the natural-phased lighting system was less likely to elicit fast-start behaviours and permitted fish to exhibit distinctive diel activity patterns.

Chandroo's (2000d) thesis also included a paper on transportation effects on adult rainbow trout (Chandroo *et al.*, unpublished manuscript). The authors recorded EMG activity before, during and after transport and provide the first data on the real-time behaviour and energetics of fish during transport. During transport, fish were extremely active as evidenced by heightened and variable EMG activity. In a similar type of study, researchers (Hennyey 1999; see Fig. 2 in Cooke *et al.* 2000c) examined the effects of different levels of anaesthetic (clove oil) on the swimming activity of adult rainbow trout during transport. In that study, the authors determined that at very low concentrations, the partially anaesthetized fish lost equilibrium and spent the majority of the time during transport attempting to regain equilibrium and thus expending substantial energy. Some research involving EMG telemetry has also been directed towards comparing the reproductive energetics of wild, farmed and sea-ranched Atlantic salmon (Einum 2002; see discussion under Reproductive ecology).

An interesting recent use of EMG telemetry is to develop an 'intelligent fish-feeding system' (McFarlane *et al.* 2002). The premise for this application is that fish with different levels of satiation exhibit different activity patterns. If the activity patterns of sentinel fish in aquaculture facilities can be used to determine the time and rates of feeding, EMG activity patterns indicative of hunger can be used to trigger automated feeders. Such a system could maximize growth rates and reduce wastage of food and the associated economic and environmental costs. This field of research will likely see rapid growth as aquaculture becomes an increasingly important sector of the regional and global economies. If EMG transmitters were to be broadly applied to production aquaculture, a standardized methodology would be required to facilitate ease of use and to provide relevant information. Some of the standardized methods outlined in this synthesis (see discussion under Generalized surgical procedure) will be useful for developing standardized techniques for use in aquaculture production facilities.

Recent research has been focused on developing welfare correlates for fish in aquaculture facilities. Chandroo (2000a) detailed the construction of a fish welfare index for rainbow trout that incorporated objective and quantifiable data obtained from EMG transmitters. Chandroo (2000a) argued that EMG telemetry incorporates measures of both behaviour and physiology that are relevant to the overall health and well-being of a given fish. He discusses the possible implications of elevated, depressed, variable or static EMG activity as indicators of change in organismal well-being. He also suggests that using EMG telemetry to identify a fish's position within its scope for activity may also prove to be useful for the assessment of fish welfare. Although the welfare index proposed by Chandroo (2000a) requires validation, the use of EMG data as a surrogate for fish welfare represents an important development in aquaculture and animal welfare research.

Catch and release

At present, only four studies have used EMG transmitters to assess the effects of catch-and-release angling. Cooke *et al.* (2000c) plotted the EMG activity of a smallmouth bass angled in a laboratory environment to preliminarily illustrate the capability of this technology for quantitatively contrasting the interspecific variation in fighting ability of hooked fishes.

Smeddes (1997) exposed hatchery adult rainbow trout to air for different durations and monitored postrelease activity in indoor tanks. Fish exposed to air for extended periods exhibited heightened activity for several hours postrelease.

Cooke *et al.* (2000b) used EMG transmitters to look at the effects of catch-and-release angling on nesting male largemouth bass. Following angling, none of the nesting fish abandoned their nests. However, activity levels of nesting fish were reduced by 40% over preangling levels more than 24 hours after capture, whereas non-nesting fish resumed normal activity levels within 1 hour of angling. This information supplemented previously collected data on the physiological condition of nesting fish postangling and illustrated how those physiological disturbances can result in potential fitness impairments.

To evaluate the behaviour of fish in livewells (aerated tanks for fish holding) during retention in competitive angling events, Cooke *et al.* (2002c) used EMG transmitters implanted in smallmouth bass. Four different density treatments were applied following the exhaustive exercise of the fish. Smallmouth bass that were held alone or with one additional bass exhibited low activity following an initial period of heightened activity when the fish were first introduced into the livewell. Conversely, densities of four or six fish resulted in heightened and variable activity throughout the livewell retention period. Cooke *et al.* (2002c) supplemented this data on locomotory activity with assessments of cardiovascular physiology. Heart rate and cardiac output generally exhibited the same trends observed with activity transmitters. From these results, the authors inferred that higher densities result in hyperactivity, which may elevate metabolic rates and increase livewell oxygen demand.

In a perspective article, Cooke *et al.* (2002a) discussed extensively the role of different physiological telemetry devices in studying marine catch-and-release issues. Although the current EMG transmitter does not function in marine environments, the authors highlighted how freshwater studies had benefited from the incorporation of EMG telemetry.

Limitations

Some of the limitations associated with EMG telemetry are actually ubiquitous among all telemetry studies. For example, it is important to ensure that the surgical procedure and/or presence of the transmitter do not disrupt the behaviour or physiology of the organism. The issue of transmitter effects was discussed earlier, and it is generally concluded that EMG transmitters do not affect behaviour. However, EMG transmitters undoubtedly have the potential to negatively affect fish, and this potential varies with species, life stage and fish size. We therefore encourage more researchers to validate this assumption as part of their projects. We also encourage the continued efforts to develop smaller batteries with longer life expectancies that will permit the use of EMG telemetry on smaller species or life stages, and for longer periods of time. Another common limitation is the cost associated with telemetry. EMG transmitters (US$500) are much more expensive than conventional transmitters (~US$150), but clearly, there are data that would be quite difficult to collect without using EMG transmitters. In many instances, the advantages of using EMG transmitters outweigh the added cost.

EMG transmitter design limits the ability to replace the battery when the factory-installed battery expires (generally 4 months). Using appropriate electronic tools and patience, additional battery life may be provided by attaching a new battery. The transmitter epoxy near the battery terminals must be removed to expose the battery contacts. The old battery should be isolated from the circuit by cutting the battery leads. Unfortunately, the epoxy and electronics preclude the actual removal of the expired battery. A series of new battery leads can be soldered to the battery terminals. These leads are then epoxied in place. Different-sized 3.6-V batteries can then be readily attached to the new battery leads. The entire transmitter package can then be waterproofed using a biologically inert material such as plasti-dip (Plasti-Dip International, Blaine, MN, USA). Transmitter performance is not altered by changing the battery and the life of the battery can be extended for longer periods with duration dependent upon battery size.

One of the biggest limitations of EMG telemetry has to do with using EMG transmitters to answer questions that could be addressed better using other approaches. These concerns usually have to do with estimating the energetic costs of different activities that result in the acquisition of an oxygen debt. For example, EMG transmitters can contribute little to assessing the energetic costs of angling after release, but can provide important information on behavioural alterations. Following release, many fish may remain motionless while the oxygen debt is repaid (Scarabello *et al.* 1991). Oxygen consumption estimates based upon EMG activity signals would suggest that the metabolic rate is depressed, when in fact, it is elevated. For this reason, Anderson *et al.* (1998) concluded that activity telemetry has limited utility for studies of catch-and-release angling. This technology, however, could be useful for monitoring catch-and-release impacts where locomotory activity displayed by fish is particularly relevant to the life history of a species (e.g. migrations, parental care, ram-obligate ventilators). It is possible to add an anaerobic 'tax' as has been done by Rand and Hinch (1998) for all swim speeds (assessed by EMG telemetry) above a certain threshold. This is a developing research area that is currently fraught with assumptions (see Burgetz *et al.* 1998).

Another example involves quantifying behaviours of free-swimming fish that are relevant to ethology and energetics, but not quantifiable using EMG transmitters. For example, in parental care-providing fish, EMG telemetry can only quantify defence behaviours that involve a locomotory response. Nonlocomotory behaviours such as yawns may be used to discourage other fish from approaching, thereby minimizing possible future energetic costs or physical injury. The energetic costs of such acts are minimal in comparison to a bursting action where the fish chases predators from the nest area. However, in some instances, the occurrences of these inexpensive defence behaviours may be important, especially in reducing the frequency of more costly behaviours. In instances such as this, it would be beneficial to combine EMG telemetry studies with observations collected using snorkelling or videography.

Difficulties associated with calibration of EMG transmitters can definitely also be viewed as limitations, particularly as it relates to applying calibrations from one group of fish to another (see under Calibration and analysis and Geist *et al.* 2002). As this was discussed in detail above, we simply wished to highlight the fact that this limitation is pervasive in the literature and requires additional efforts directed at understanding the error associated with not calibrating all transmitter-carrying fish. More information is also required on the absolute costs and muscle recruitment characteristics for fish with different modes of locomotion. Although we spent significant effort attempting to make EMG technology accessible to new users, it is important to understand the fundamental ecomorphological and physiological factors that underlie the muscle function and swimming. The calibration procedure is an essential step to estimate the energetic costs of locomotion, and greater efforts must be placed on understanding what can reasonably be extended from calibrations to the field. There is much opportunity to undertake studies that contrast different calibration techniques including those that are not based solely on forced steady-state, linear swimming in a respirometer.

There are currently few examples where EMG telemetry data have been coupled with other indicators of metabolic rate or physiological disturbance. Studies that integrate conventional laboratory measures of metabolic disturbance using blood and tissue assays with field studies using remote collection of physiological and behavioural parameters of free-swimming fish will provide the most comprehensive and relevant data for the conservation and management of fisheries. An example of such a study was conducted in several marine species (sole, *Solea solea*, Soleidae; and European sea bass, *Dicentrarchus labrax*, Moronidae) by Sureau and Lagardére (1991). In that study, the authors coupled heart-rate telemetry with locomotory activity telemetry. For sole, the heart rate and locomotory activity were correlated whereas for sea bass, those variables were not. Cooke *et al.* (2002c) also combined EMG telemetry with hard-wired cardiac output monitors to assess the energetic costs of livewell confinement on smallmouth bass. To our knowledge, there are no studies that have conducted any biochemical assays on EMG-transmitter-implanted fish. Similarly, there are no examples where researchers have conducted proximate body composition on fish that have been implanted with EMG transmitters. Although several studies have examined energetic status on other parallel individuals, it would be useful to nondestructively assess energy status at the time of implantation and then again after some period of time on the tagged individuals. This would serve as an important validation and could identify any disparities between EMG telemetry and other energetic assessments. Linking individual behaviour with physiology by coupling nonterminal blood sampling with EMG transmitter implantation may provide an important tool for understanding interindividual variation.

For some researchers, especially muscle physiologists, one of the largest limitations of the EMG transmitter is the fact that it only provides a relative indicator of EMG activity. This is generally not of concern for those interested in activity and energetics questions, but it does limit the use of these transmitters in detailed physiological assessments of muscle activation timing, changes in fibre recruitment patterns, muscular efficiency and power output (Bone *et al.* 1978). The raw EMG transmitter that monitors the full EMG waveform designed by Dewar *et al.* (1999) is more appropriate for those types of studies. Confirmational studies by Beddow and McKinley (1999) illustrate that for Atlantic salmon, EMG telemetry can be used to quantify the relative muscle activity of fish and serve as an index of swimming speed and energetics.

As EMG transmitters incorporate a radio output module, it is currently not possible to use EMG transmitters in deep water or marine environments. Radio signals are quickly attenuated by deep or highly conductive water. An important development would be the addition of a factory option for purchasing either ultrasonic or radio versions of the EMG transmitter. This would greatly expand the utility of these transmitters and may actually help to promote their widespread adoption. This serious limitation should be remedied. An alternative approach may be the development of an archival EMG transmitter that stores data for later download. This approach may be particularly useful for fish that occupy habitats that are not conducive to manual tracking or the use of a fixed telemetry array.

Although we have outlined some serious limitations with EMG telemetry, most of these can be remedied through continued technological advances, through consideration of other techniques for instances when EMG telemetry will be ineffective for addressing the desired research question, and through continued research on the basic performance of EMG transmitters in a range of different fish and environments. As we have just presented a list of limitations with using EMG telemetry, it is perhaps also appropriate to briefly highlight the advantages of EMG telemetry. The current EMG transmitter is currently the best method of monitoring the long-term (several months) activity and energetics of free-swimming fish. The large number of applications to which EMG transmitters have been applied, and the numerous questions that have been previously unable to address, is indicative of the many benefits associated with EMG telemetry.

Prospectus and conclusions

We are strong proponents of continued research and development on the remote collection of indices of locomotory activity (and other relevant measures). To date, these technologies have been applied only sparingly to a diversity of fisheries-related problems. Although the technological and surgical skills required to use these tools has limited their widespread adoption, several laboratories in North America and Europe have used them with success. Currently, these researchers are working in isolation, helping to perpetuate the notion that only those with experience with these transmitters can have success with them. Although we use similar technology, there are many subtle differences in equipment, surgical technique and analysis that have arisen in individual laboratories. As numerous studies utilizing activity transmitters now exist illustrating a variety of different techniques for surgical implantation (see Beddow and McKinley 1999; Bunt 1999a; see Abstract in this paper), data collection and data analysis, it is intuitive to encourage the standardization of approaches to facilitate comparisons across studies. We also encourage the adoption of approaches that incorporate other indicators of an organism's physiology and behaviour. In this paper, we have provided several novel examples of how commercially available activity transmitters can be used to generate useful data. Researchers will gain the most benefit from EMG telemetry when applying this technology as part of a more comprehensive approach to address a specified set of objectives rather than designing experiments to use EMG telemetry.

When EMG telemetry is combined with other more conventional methodologies, scientists will have a robust set of tools to integrate both behaviour and physiology in understanding how fish respond to different stressors and how they interact with other organisms and their environment. Behavioural studies only provide information on what animals are doing. An understanding of the proximate basis for a given behaviour, i.e. how they are physiologically able to perform the activity, is essential to understand ultimate questions of why they behave as they do. EMG transmitters have the possibility of providing information on both the proximate and ultimate basis of behaviours. Although the focus of this paper was 'fisheries science', EMG telemetry has the potential to contribute to advances in ecological and evolutionary theory through the execution of well-designed field studies. Indeed, research on marine mammals (e.g. Butler 1989) and birds (e.g. Butler and Woakes 1982) that have utilized physiological telemetry to address questions at the interface of behaviour and physiology have clearly helped to elucidate and understand mechanisms and relationships between animals and their environment. Ecologists that use fish as models could benefit from the widespread acceptance of EMG telemetry (and other forms of physiological telemetry; see Lucas *et al.* 1993) as an important tool in ecological and evolutionary research.

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