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Swimming speeds and metabolic rates of semi-captive juvenile lemon sharks (*Negaprion brevirostris*, Poey) estimated with acceleration biologgers

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ABSTRACT

There is much interest in being able to quantify the swimming speeds and metabolic rates of wild aquatic animals such as sharks to develop bioenergetics models and evaluate the metabolic consequences of different stressors. This study sought to calibrate tri-axial acceleration biologgers (accelerometers) such that it would be possible to estimate swimming speeds and metabolic rates of semi-captive sharks in an enclosed natural mesocosm. Juvenile lemon sharks (*Negaprion brevirostris*, Poey; 60–75 cm total length, 1–2 kg) were equipped with accelerometers and swum at stepwise velocity increments in a Blazka-style swim tunnel respirometer using a critical swimming speed protocol. Metabolic rates and acceleration-derived metrics (overall dynamic body acceleration and tailbeat frequency) were measured concurrently during forced swimming, and accelerometer-equipped sharks were released to an enclosed mesocosm habitat to estimate average daily metabolic rate (ADMR) and swimming velocities across diel and tidal cycles. Acceleration-derived tailbeat frequency was a stronger predictor of metabolic rate than overall dynamic body action, and predicted an active metabolic rate of 249.7 ± 1.9 mg O_2 kg^{-1} h^{-1} and an ADMR of 88.7 ± 0.7 kJ kg^{-1} d^{-1} at 30 °C. Following exhaustive exercise a maximum metabolic rate of 398.0 ± 19.6 mg O_2 kg^{-1} h^{-1} was achieved and over the subsequent 55-minute recovery period excess post-exercise oxygen consumption was 31.2 mg O_2 kg^{-1}. The critical swimming speed of the sharks was 0.71 ± 0.03 body lengths per second (BL s^{-1}), and swimming speed in the mesocosm was 0.19 ± 0.01 BL s^{-1}. Locomotor activity levels of semi-captive sharks in the mesocosm were influenced by tide state and diel period, with sharks having highest swimming velocities during diurnal periods and flooding tides. Overall, accelerometry is a suitable means for estimating swimming speed and metabolic rate in this species, and additional research to address anaerobic energy expenditure of wild sharks is warranted.

1. Introduction

Understanding rates of energy expenditure in wild fishes (i.e., swimming speeds and metabolic rates) is important for estimating how energy use changes when fishes are exposed to environmental or anthropogenic stressors (Treberg et al., in press). Elasmobranchs were initially thought to have the lowest metabolic rates and activity levels of all fishes (Brett and Blackburn, 1978), though evidence suggests that elasmobranchs have comparable metabolic capacities as ecologically similar teleosts (e.g., Bushnell et al., 1989; Dickson et al., 1993; Lowe, 2001). Several studies have addressed the effects of mass and temperature on aerobic metabolic rates (e.g., Dowd et al., 2006; Whitney et al., 2016), fewer address conservation issues (e.g., Barnett et al., 2016), and only one has addressed anaerobic energy expenditure (Brett and Blackburn, 1978). Elasmobranch studies, however, are advancing to the point where they have begun to elucidate patterns in metabolism across species with different "pace-of-life" traits (e.g., Whitney et al., 2016). For instance, inactive

Abbreviations: ADMR, average daily metabolic rate; EPOC, excess post-exercise oxygen consumption; MMR, maximum metabolic rate; ODBA, overall dynamic body acceleration; RMR, resting metabolic rate; SMR, standard metabolic rate; TBF, tailbeat frequency.

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species typically have very low metabolic rates (e.g., Whitney et al., 2007, 2016), whereas obligate ram-ventilating species have considerably higher metabolic rates attributed to the increased costs of maintaining larger gill surface area (Bernal et al., 2012). Thus, while studies are beginning to define trends in aerobic metabolic performance, the understanding of the anaerobic performance of sharks is limited (Bernal et al., 2012). Studies have estimated metabolic rates of wild sharks using laboratory defined relationships between metrics of energy expenditure and activity, but a comprehensive picture of the activity metabolism of wild sharks is incomplete without understanding an animal's full aerobic and anaerobic capacities (Whitney et al., 2016). Therefore, quantifying metabolic rates and activity levels in wild sharks will improve estimates of changes in energy use in response to environmental or anthropogenic stressors.

Comprehensive laboratory and field metabolism studies would ultimately allow researchers to provide ecologically meaningful estimates of metabolic rates that could be used to address energy requirements of populations and address conservation issues (Treberg et al., in press). Studies that incorporate a field component to "bridge the gap" between the laboratory and field are lacking for sharks, partially owing to logistically difficulties associated with shark respirometry and that a single method to remotely measure metabolic rates and activity levels has not been universally adopted (Lowe and Goldman, 2001). Metabolic rates are typically measured indirectly as rates of oxygen consumption using respirometry, though the logistics of respirometry can be prohibitive for many species (Bernal et al., 2012). In general, shark respirometry studies have been limited by the size of the animal that commercially available respirometers can accommodate (e.g., Graham et al., 1990) and whether the animal is an obligate ram-ventilator, because measurement of standard metabolic rate (SMR, the metabolic rate of a fasted shark at rest and stable temperature; Chabot et al., 2016) and excess post-exercise oxygen consumption (EPOC, the mass of oxygen consumed above SMR to restore anaerobic substrates and resolve physiological disturbance after exhaustive activity; Gaesser and Brooks, 1984) require that sharks are motionless (e.g., Dowd et al., 2006). Furthermore, swimming sharks at a range of activity levels necessary for sensor tag calibration can be further complicated by confinement stress from respirometers (e.g., Lowe, 1996, 2001) or uncooperative behavior of the study species (e.g., Whitney et al., 2007, 2016). Where researchers have been successful, however, studies have provided key insights into basic animal ecology (e.g., Lowe, 2002; Sundström and Gruber, 1998), and have addressed changes in diel energy expenditure owing to anthropogenic stressors (e.g., Barnett et al., 2016). While metabolic rates measured for captive animals can be extrapolated to estimate energy requirements of wild animals, combined laboratory and field studies ultimately provide ecologically meaningful estimates of energy requirements.

Acceleration biologgers (accelerometers) are a valuable tool that may help to bridge the gap between laboratory and field studies of elasmobranch metabolism (Whitney et al., 2012; Cooke et al., in press). Specifically, acceleration-based metrics provide high resolution and fine-scale behavioral measurement (Brown et al., 2013), and are activity-specific proxies for expenditure in free-ranging animals (e.g., Halsey et al., 2009b). The metric overall dynamic body acceleration (ODBA; Wilson et al., 2006), which assumes energy expenditure scales linearly with acceleration generated from muscle contraction (Gleiss et al., 2011), correlates metabolic rates with activity (Wilson et al., 2006) and has been validated for scalloped hammerhead sharks (*Sphyrna lewini*; Gleiss et al., 2010). While ODBA is a promising proxy of energy expenditure, studies have questioned whether logging acceleration at high frequencies in three axes is any better than logging in fewer axes because of the associated memory and battery requirements (Halsey et al., 2009a). In addition to ODBA, tailbeat frequency (TBF) can be derived from acceleration in the lateral axis of movement (Kawabe et al., 2003), and has previously been used to quantify metabolic rates and swimming speeds in sharks using a tailbeat-sensing acoustic transmitter (Lowe, 2002; Lowe et al., 1998). Studies have recently begun to apply accelerometry for shark research to determine its suitability for remote behavioral (Whitney et al., 2007; Wilson et al., 2015) and physiological (Gleiss et al., 2010) assessments, yet few have applied accelerometry to define activity-specific metabolic rates for elasmobranchs (Barnett et al., 2016). Given the capacity for accelerometers to measure behavior and estimate rates of energy expenditure, accelerometry should be capable of bridging the gap between field and laboratory studies of elasmobranch metabolism.

The primary objective of this study was to telemeter activity levels in semi-captive lemon sharks (*Negaprion brevirostris*, Poey) to estimate metabolic rates, swimming velocities, and diel energy expenditure, using laboratory calibrations of metabolic rates with acceleration-derived activity metrics using swim tunnel respirometry. A secondary objective was to quantify recovery of sharks from the exhaustive exercise protocol employed for calibration in an attempt to incorporate anaerobic metabolic costs into metabolic rate estimations by measuring EPOC. Lemon sharks were selected as the study species because lemon shark metabolism has been well documented relative to other elasmobranchs, including several studies that sought to calibrate metabolic rate with various sensor tags (e.g., heart rate: Scharold and Gruber, 1991; speed-sensing tag: Sundström and Gruber, 1998). Furthermore, studies have begun to validate the use of accelerometry for remote behavioral measurement, and have suggested that accelerometry is a promising method for metabolic rate measurement in lemon sharks (Gleiss et al., 2009). Therefore, the use of this species allows for comparison with previous metabolism and telemetry studies.

2. Materials and methods

All research was conducted under research permits MAF/FIS/17 and MAF/FIS/34 issued by the Bahamian Department of Marine Resources and followed the Cape Eleuthera Institute (CEI) animal care protocols based on guidelines set forth by the Association for the Study of Animal Behavior and the Animal Behavior Society (Rollin and Kessel, 1998). Permission to capture sharks within the Bahamian Shark Sanctuary was established in accordance with Bahamian Department of Marine Resources Form 20A, Regulation 36D (3), permitting fishing, possession, and exportation of sharks or shark parts.

2.1. Animal collection and husbandry

Sharks were collected from tidal mangrove creeks around Cape Eleuthera, Eleuthera, The Bahamas (24°49′46.43″N, 76°19′41.49″W) between 31 March and 8 August 2014 for laboratory calibration, and between 31 August and 22 September 2014 and 2–4 June 2015 for field deployments. All animals were captured using seine netting and brought back to CEI's wet lab within 45 minutes post-capture. During transit, half of the water in holding totes was replaced every 5 min to provide adequate aeration and quality (Brooks et al., 2011). Sharks were maintained in a 13,000 L (3.7 m diameter by 1.25 m depth) open-circulating tank continuously aerated and supplied with fresh seawater. The wet lab is an open-sided, covered, outdoor facility exposing animals to ambient seasonal water temperatures and a natural photoperiod. Feeding occurred daily and consisted of one thawed commercially available Spanish sardine (*Sardinella aurita*) per shark. All sharks were acclimatized to wet lab conditions for at least three days prior to use in experiments.

2.2. Acceleration measurement

To quantify activity, lemon sharks were fitted with an accelerometer (X8M-3, Gulf Coast Data Concepts, Waveland, MS, USA; 5.1 cm × 2.5 cm × 1.3 cm, 17 g; 25 Hz recording frequency; ±8g acceleration range), secured to plastic frontal and backing plates