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Estimates of field activity and metabolic rates of bonefish (*Albula vulpes*) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry

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ABSTRACT

We tested the utility of acoustic tri-axial acceleration transmitters in combination with ethogram and respirometry studies to quantify the activity patterns and field metabolic rates of free-swimming bonefish (*Albula vulpes*) in the coastal waters of Eleuthera, The Bahamas. Bonefish were found to exhibit relatively low activity levels in the field with no evidence of diel patterns or inter-sexual variation. Low activity levels reported by the accelerometers reflected low swimming speeds and intermittent swimming behaviours (i.e., swim-then-drift) that maximized energy efficiency. Such behaviours were also observed when conducting ethograms on bonefish held in a large field mesocosm. Laboratory derived standard metabolic rates and maximum metabolic rates during recovery from exercise were combined with acceleration transmitter calibrations to determine that individual bonefish typically operate at between 40 and 60% of their estimated metabolic scope in the field. However, occasionally acceleration values in the field were indicative of high intensity bursting activity that exhausted the majority of their estimated metabolic scope (0.7% of all field observations exceed 90% of estimated metabolic scope). Data gathered in this study provide a critical starting point for the development of a bioenergetics model for bonefish which will ultimately lend clues into how fish make a living in tropical tidal flats environments. Given that this paper is one of the first to use transmitters rather than archival loggers to collect data on tri-axial acceleration on fish, we also discuss the opportunities and limitations of using this new technology for marine fisheries research.

1. Introduction

Energy is an important commodity for all organisms, and is the currency most often employed in analyses of animal behaviour (Townsend and Calow, 1981). How animals partition energy into different life functions, and thus how they make a living, can be represented by balanced energy equations (Soofiani and Hawkins, 1985). Animals making energetic choices that increase survival will be favored, and as such, the balanced energy equation is strongly influenced by natural selection (Diana, 2004; Wilson et al., 2006). Estimating the complete energy budget of a free-living organism, however, has presented challenges to scientists, particularly when assessing the energetic costs of activity in fish (see Briggs and Post, 1997a). As the cost of activity may represent a large and variable component of the fish's energy budget (Boisclair and Sirois, 1993), the methods used to measure locomotion need to be effective in free-swimming fish in the wild (Briggs and Post, 1997b; Cooke et al., 2004).

Previous studies have explored the utility of a variety of biotelemetry sensors including heart rate (e.g., Lucas et al., 1991), tail-beat frequency (e.g., Ross et al., 1981), and axial muscle electromyograms (EMGs) (e.g., Briggs and Post, 1997a,b; Cooke et al., 2004). However, both heart rate (electrocardiogram (ECG)) and EMG transmitters require precise surgical implantation of electrodes and significant handling of the animal (Whitney et al., 2007). More recently, the use of animal-borne acceleration data loggers for studying free-swimming fish and other animals is gaining popularity (Wilson et al., 2007; Shepard et al., 2008). Because locomotion occurs when animals expend energy to contract muscles which leads to body acceleration, the accurate measurement of acceleration should be a good proxy for energy expenditure during activity (Halsey et al., 2009). Indeed, acceleration data loggers have been successful in elucidating homing migrations and spawning behaviour in salmon (Tanaka et al., 2001; Tsuda et al., 2006; respectively), diel activity patterns in whitetip reef sharks (*Triaenodon obesus*) (Whitney et al., 2007), and general activity

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patterns in rainbow trout (*Onchorhynchus mykiss*) (Kawabe et al., 2003a) and Japanese flounder (*Paralicthys olivaceus*) (Kawabe et al., 2003b). Acceleration data loggers have their limits as well, requiring retrieval of the logger to access the data (Ropert-Coudert and Wilson, 2005). Only recently has the technology of onboard processing improved sufficiently to encode and transmit tri-axial accelerometer data efficiently. With acceleration transmitters the data are sent to acoustic hydrophone receivers, extending the use of these devices to species and/or environments where recaptures are difficult.

Knowledge of the activity patterns and energetic requirements of marine species is becoming increasingly important for modeling ecosystems and managing populations (Lowe, 2002; Fitzgibbon et al., 2007). This is particularly true for species occupying coastal habitats, since over half of the world's population lives in these areas (Barnabé and Barnabé-Quet, 2000). Habitat degradation is widespread where humans exploit resources such as mangrove forests (Alongi, 2002; Blaber, 2007). Studying the behaviour and activity patterns of a species that not only occupies coastal marine environments, but is also the object of an economically important recreational fishery may provide insight into individual and population level processes, which may ultimately influence the effectiveness of conservation and management strategies.

Bonefish (*Albula* spp.) are a group of benthivorous fish found in tropical tidal flats and tidal creeks (Colton and Alevizon, 1983a,b; Humston et al., 2005). Throughout much of their circumtropical distribution bonefish also carry the distinction of being a popular sport fish and thus play an important role in many local economies (Pfeiler et al., 2000; Ault, 2008; Danylchuk et al., 2008). To date, there has been no known study which has examined bonefish activity patterns and behaviour beyond traditional positional biotelemetry studies (see Colton and Alevizon, 1983b; Humston et al., 2005; Friedlander et al., 2008; Larkin et al., 2008), all of which have had limited spatial (often on the order of 500 m accuracy of positioning) and temporal resolution (fish tracked at infrequent intervals and often for short duration), making it impossible to evaluate fine-scale activity patterns or estimate energy expenditure.

The objective of this study was to quantify the field activity and metabolic rates of bonefish (*Albula vulpes*) in tidal flats and tidal creek areas near Cape Eleuthera, Eleuthera, The Bahamas. Using acoustic tri-axial acceleration transmitters, we investigated the influence of sex and photoperiod on the activity patterns of wild bonefish and compared results to laboratory and field calibrations. Furthermore, we catalogued the discrete behaviours of bonefish held in a natural wetland mesocosm to produce an activity time budget. Static respirometry was used to determine standard metabolic rate and maximum metabolic rate during recovery after exercise. When combined with data from accelerometers, we estimated the field energetics of bonefish.

2. Methods

2.1. Study site

This study was conducted along a 15 km section of the north coast of Cape Eleuthera, Eleuthera, The Bahamas (N 24° 50′ 05″ and W 76° 20′ 32″), as well as the Cape Eleuthera Institute (CEI) research facility (Fig. 1). The coastline in this area is composed of tidal creeks, sandy bays, mangroves, and jagged calcium carbonate outcroppings. Preliminary genetic analyses on bonefish from this area indicated that all specimens were *A. vulpes* (Danylchuk et al., 2007). All procedures used in this study were in accordance with the policies of the Canadian Council on Animal Care as administered by the Carleton University Animal Care Committee (Protocol B07-03, B07-05, and B07-06).

2.2. Acceleration transmitter experiments

On December 8, 2008, 10 bonefish (527 ± 36 mm total length; mean ± SD) were implanted with acoustic tri-axial acceleration transmitters. Water temperatures were 22.5 °C at time of capture. The transmitters (model V9AP-2L coded tags, 46 mm long, 3.3 g in air, 160 day battery life; Vemco Inc., Shad Bay, NS.) measure acceleration in the *X*, *Y*, and *Z* axes at a rate of five samples per second with a 25 second sampling period. This model of tag calculates a value (vector, measured in g-force) that represents the root mean square of acceleration from each of the three axes over time (i.e., $\text{g}-\text{force} = \sqrt{x^2 + y^2 + z^2}$). The value in g-force is converted to m/s^2 by multiplying by 9.8. The transmitter was programmed to transmit randomly at an interval ranging from 45 to 135 s, with an average of 90 s. The transmitters alternated in the transmission of acceleration and depth information, however the depth data were not used in the current study as most hydrophones were placed in shallow waters (i.e., <2 m).

To capture bonefish for implantation with the acceleration transmitters, various sized seine nets were deployed at the mouth of a tidal creek

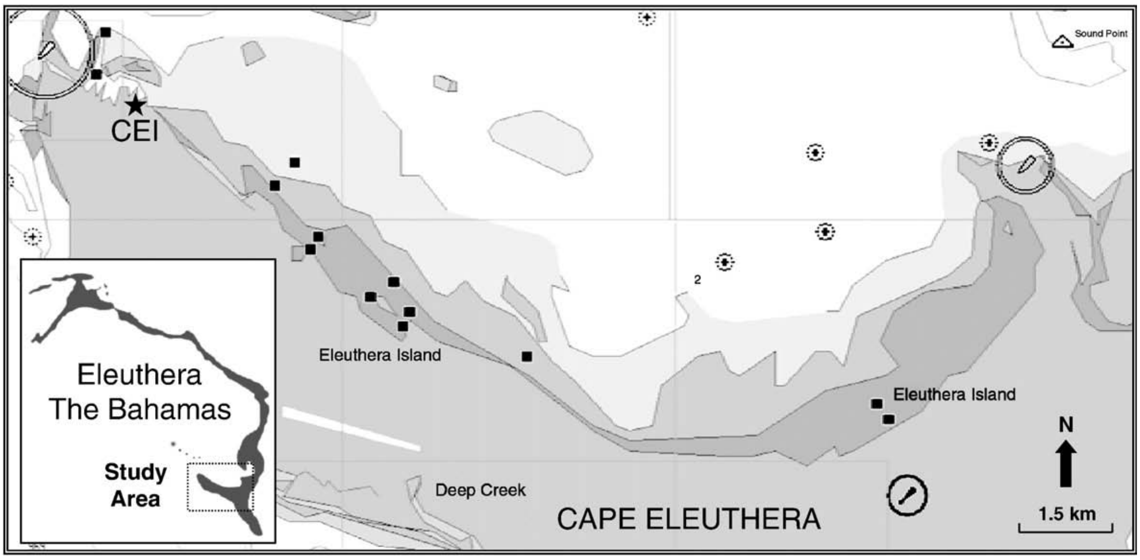

Fig. 1. Study area along the north coast of Cape Eleuthera, Eleuthera, The Bahamas, showing the locations of the 13 hydrophone receivers (black squares), and the location of the Cape Eleuthera Institute research facility (black star). The inset map displays the entire island of Eleuthera with the study area highlighted.

to intercept fish on an outgoing tide (as per Murchie et al., 2009). When a school of bonefish approached, the net was moved quickly to encircle the fish. Captured bonefish were dip-netted or passed by hand into flow-through holding pens (1.3 m × 0.8 m × 1.25 m, 3.1 cm extruded plastic mesh) submerged in a minimum of 0.6 m of water where they were held until surgery. Bonefish were anesthetized with MS-222 prior to surgery (approximately 100 ppm) and then placed on a surgery table where the gills were supplied with a maintenance dose of MS-222 (approximately 50 ppm) in recirculating seawater. To implant the transmitter, a small (2–3 cm) incision was made to one side of the ventral midline, posterior to the pectoral fins. After being disinfected with an iodine solution, the transmitter was inserted and gently guided into the coelomic cavity, toward the pectoral fins. The transmitter was always oriented the same way for each fish (i.e., accelerometer sensors facing anteriorly). The incision was closed with 3–4 simple interrupted sutures using monofilament absorbable suture material (Ethicon 3-0 PDS II, Johnson and Johnson, New Jersey). The length of the fish (mm) was measured, and the sex was determined via internal examination. The entire procedure generally took less than 5 min. Bonefish were held for up to 1 h in the flow-through net pens to recover following anesthetization. Transmitter-implanted fish were released simultaneously with a group of untagged bonefish (at least $n = 10$) from the same school from which they were captured. All surgeries were completed by the same surgeon who had previously implanted more than 2000 telemetry devices in fish.

A series of 13 hydrophone receivers (VR2 and VR2W models, Vemco Inc., Shad Bay, NS) deployed prior to December 8, 2008 were used to record acceleration values as transmitter-implanted fish swam through the study area (Fig. 1). Receiver locations covered tidal flats, the mouths of tidal creeks, and other nearshore areas bonefish have been found to frequent (Murchie, unpublished data). Individual receivers were anchored to a short piece of rebar cemented into a concrete block. Receivers in water greater than 1 m deep at low tide and in open water were positioned vertically in the water column. In water that was <1 m deep at low tide and at narrow choke points, receivers were deployed horizontally or 5–10° above horizontal, with the hydrophone orientated to maximize coverage. Range tests were performed upon the initial deployment of the receivers, revealing that receivers deployed in water greater than 1 m deep had a coverage radius of 250 m, whereas receivers in shallow water or positioned horizontally had a coverage radius as small as 30 m due to shoreline confinement. Wind and wave conditions, as well as tidal cycles, influence the detection range of individual receivers (Heupel et al., 2006). Although the range of coverage for receivers in shallow water or positioned horizontally was considerably less, they did provide the necessary coverage to monitor choke points (i.e., creek mouths) and as such we did not correct for receiver range in our data analysis. Receivers were visited regularly to download data and to clean the hydrophone of biofouling material. Data were collected for the duration of the transmitter battery, or until the fish died or left the study area. Temperature data collected from a data logger (Hobo-H8 temperature logger, Onset Computer Corporation, ±0.7 °C accuracy, range of −20 °C to 70 °C) encased in a waterproof housing just offshore of CEI revealed the mean water temperature in the field between December 8, 2008 and June 1, 2009 was 23.7 ± 2.5 °C.

To determine the range of acceleration values that could be generated for implanted bonefish, a laboratory calibration was conducted. Additional bonefish ($n = 17$) captured by seine net on December 8, 2008 were transported to the CEI research facility following protocols outlined in Murchie et al. (2009). Fish were held in large (3.7 m diameter × 1.25 m height; 13 180 L) circular holding tanks that were aerated and continuously supplied with fresh sea water (1800 L/h) at ambient temperatures. Tanks were housed in a covered open-sided outdoor facility with natural photoperiod, but the tanks themselves were uncovered. Bonefish were maintained on a diet of sinking pellets (13 mm Zeigler, USA) (Murchie et al., 2009). Seven laboratory-acclimated bonefish (419 ± 17 mm total length; mean ± SD) were implanted with acceleration transmitters (as described above) between January 14 and January 17, 2009, and were left to recover from surgery in a smaller holding tank (1.6 m diameter × 0.85 m height; 1400 L) for a minimum of 12 h before experimentation. Acceleration values for swimming, bursting, and stationary behaviours were generated. Swimming values were determined for all seven bonefish by using a VR100 portable receiver (Vemco Inc., Shad Bay, NS) and VR110 hydrophone to log transmitted acceleration data while bonefish swam leisurely in the holding tank for a minimum of 30 min. Each bonefish was then captured and placed individually in an inflatable children's wading pool (1.5 m wide, 19 cm deep) with the portable hydrophone. Once a depth transmission occurred, which is visible on the VR100, bonefish were chased by tail grabbing (Suski et al., 2007) to provoke them to burst. Bonefish were chased in this manner until the acceleration transmission occurred (approximately 2 min on average). After being chased, bonefish rested in the pool and stationary values were recorded. Two burst and two resting values were recorded for each of the seven fish. Because there were only three accelerometer transmitters to be used between the seven fish for calibration, four bonefish had to be euthanized with a lethal dose of MS-222. An additional stationary value for dead bonefish was recorded and the transmitter removed.

The last three bonefish implanted with acceleration transmitters were marked with T-bar anchor tags in unique colour combinations and then released into a natural wetland mesocosm after their calibration values were recorded. The wetland is immediately adjacent to CEI and receives water continuously (approximately 1900 L/h) discharged from a flow-through wetlab facility. The total area of the wetland is approximately 250 m^2 and is vegetated primarily with red mangrove (*Rhizophora mangle*) and black mangrove (*Avicennia germinans*). The wetland is also intermittently connected to the ocean during spring tides and fish enter the system at that time. Typical inhabitants include schoolmaster snapper (*Lutjanus apodus*), yellowfin mojarra (*Gerres cinereus*), juvenile great barracuda (*Sphyraena barracuda*), as well as a variety of small-bodied fish species, and one young-of-the-year lemon shark (*Negaprion brevirostris*). Six bonefish were introduced in the wetland in September 2007 to determine whether the wetland could be used as a potential mesocosm. The fish thrived and were all alive in January 2009 suggesting the wetland was a suitable habitat. The three acceleration transmitter-implanted bonefish were introduced to their conspecifics in the wetland on January 17, 2009. The fish immediately joined the schooling resident bonefish. The bonefish typically remained in the deepest section of the wetland (approximately 0.5 m) which was close to 25 m^2. On January 29, 2009 a VR2W receiver was placed in the wetland to record acceleration values from the three tagged fish. The receiver was positioned vertically by burying it in the substrate so only the top 20% of the receiver was visible. Acceleration data were collected from January 29 to May 19, 2009.

2.3. Ethogram study

Although it is not typically possible to observe detailed bonefish behaviour for long periods of time in the wild, the wetland provided an ideal environment to develop an ethogram for bonefish. A wooden foot-bridge stretched across the width of the wetland and was directly adjacent to the deepest area where the bonefish most often resided. From the bridge, an observer could easily watch the behaviour of the school or isolate the behaviour of an individual. Unfortunately the coloured sheath of the T-bar anchor tags on two of the acceleration transmitter-implanted bonefish fell off within a few days of release, but the anchor tags on the third fish remained. Between January 19, 2009 and January 24, 2009, bonefish were observed for a total of 3 h to determine their distinct behaviours. Focal sampling (see Martin and Bateson, 1993) of the remaining marked bonefish (i.e., the one with the remaining T-bar anchor tags) occurred for 10 minute intervals during 20 morning (7:10–9:20), 20 noon (11:33–13:13), and 20 pre-dusk (17:41–18:52) monitoring periods between March 25, 2009 and May 15, 2009. During the observation period, the order and duration of specific behaviours was recorded.

2.4. Respirometry study

Because the basis for metabolism is the conversion of glucose and oxygen into carbon dioxide, water and energy (Diana, 2004), determining the standard metabolic rate (SMR) and maximum metabolic rate during recovery after exercise (MMR_R) would serve as a set of metabolic bounds in which bonefish operate. Using the remaining 10 bonefish (407 ± 42 mm total length; mean ± SD) held in captivity, SMR and MMR_R were determined using computerized, intermittent-flow respirometry (LoligSystems, Hobro, Denmark) (Steffensen, 1989). The system consisted of four glass chambers (746 mm length × 140 mm wide) outfitted with fiber optic oxygen probes immersed in a tank (3.09 m length × 0.65 m width × 0.17 m height) of aerated sea water at ambient temperatures. Each glass chamber was connected to two aquarium pumps; one for recirculating water through the chamber, and one for flushing ambient, oxygenated water into the chamber. The total volume per set up, including the glass chamber, two pumps, and all associated tubing was 11.48 L. Experiments were designed such that oxygen consumption in each individual chamber was quantified within 26 minute cycles that consisted of a 10 minute measurement phase, a 15 minute flush period to replace water in each chamber, and a 1 minute wait period following each flushing prior to commencing measurements. During each measurement period, water from the chambers was continually recirculated over the fiber optic oxygen probes to ensure adequate mixing. The change in oxygen concentration (α) for each chamber was calculated as slope ($\Delta O_{2saturation}/\Delta t$), and oxygen consumption rate (MO_2, mg O_2 kg^{-1} h^{-1}) for each fish was calculated by:

$$MO_2 = \alpha V_{resp} \beta M_b^{-1},$$

where V_{resp} is the volume of each glass chamber minus the volume of the fish (L), β is oxygen solubility (adjusted daily for both temperature and barometric pressure), and M_b is the fish mass (kg) measured before placing in the respirometer chamber. During each trial, the coefficient of determination (r^2) for all slope measurements was >0.95. All calculated dissolved oxygen values were corrected for background oxygen consumptions generated for each specific fish and chamber prior to commencing experiments. Calibration of the fiber optic oxygen probes occurred with oxygen-free water and fully saturated water regularly through the experiments. Data were recorded with AutoResp software (Version 1.4, Steffensen, 1989; Schurmann and Steffensen, 1997). Fish were not fed 24 h prior to experimentation. SMR values were calculated as the average of six lowest values recorded between 20:00 and 06:00 as very minimal human disturbance occurred in the wetlab during these hours (Schurmann and Steffensen, 1997; Gingerich et al., 2010). After 06:00, individual fish were removed from their chamber, exercised continuously for 4 min by tail grabbing (Suski et al., 2007), and then put back in their chamber to measure MMR_R. MMR_R was determined as the highest value recorded over a six hour recovery period. A six hour recovery period was selected as bonefish were found to require 4 h to return to baseline blood chemistry values following exhaustive exercise (Suski et al., 2007). While the true metabolic scope (i.e., MMR-SMR) could not be calculated since a true MMR was not determined, an estimate of metabolic scope (i.e., MMR_R-SMR) was calculated and field data expressed as a percent of estimated scope as per Priede (1977). Respirometry trials were conducted between February 7, 2009 and February 12, 2009, during which the water temperature was 20.6 ± 0.7 °C.

Table 1
Summary of the tagging, biological, and monitoring data for the 10 wild bonefish implanted with acceleration transmitters and released along the north coast of Cape Eleuthera, The Bahamas, December 8, 2008.

Sex	Transmitter ID	Total length (mm)	Date last detected	# of detections
Female	128	555	15-Dec-08	495
Female	130	578	17-Jan-09	2035
Female	138	590	18-Mar-09	2865
Female	140	520	10-Dec-08	152
Female	142	515	31-May-09	6891
Male	132	475	01-June-09	3453
Male	134	510	11-Dec-08	52
Male	136	520	31-May-09[a]	2897[a]
Male	144	495	27-May-09	2766
Male	146	515	31-May-09	4434

[a] The accelerometer sensor failed in transmitter 136 and was therefore not included in the analyses.

2.5. Data analysis

All statistical analyses on collected and derived data were completed using JMP 8.0.2 (SAS Institute, Cary, NC). Maximal type-1 error rates were set at $\alpha = 0.05$. Normality and homogeneity of variance assumptions were evaluated using Shapiro–Wilk or Kolmogorov Smirnov goodness-of-fit tests and Levene's test, respectively (Sokal and Rohlf, 1995). Acceleration data derived from the wild and wetland environment were evaluated for differences in photoperiod and sex (wild only) using repeated measures analysis of variance (ANOVA). Photoperiod was divided into day (06:00–17:59) and night (18:00–5:59) and divisions were based on sunrise and sunset timing data from a weather station located on Cape Eleuthera. Linear regression was used to generate an equation of the line relating oxygen consumption to acceleration following determination of SMR and MMR_R. Mean acceleration from free-swimming bonefish in the wild was incorporated into the equation to derive an average field metabolic rate.

3. Results

3.1. Acceleration experiments

Laboratory calibration of acceleration transmitters provided baseline values to which the wild and wetland acceleration data could be compared. A dead bonefish in a cooler of water gave an acceleration of 0.06 ± 0.01 m/s^2, whereas a stationary alive bonefish had an acceleration value of 0.37 ± 0.14 m/s^2. Acceleration values for swimming (routine) and bursting bonefish were 0.60 ± 0.18 m/s^2 and

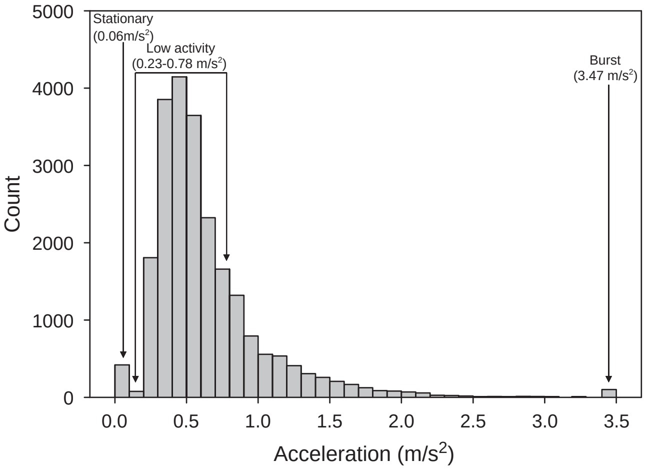

Fig. 2. Histogram of acceleration activity from free-swimming bonefish in the wild. Values for stationary, low activity, and bursting from laboratory calibrations were overlaid on the histogram for reference.

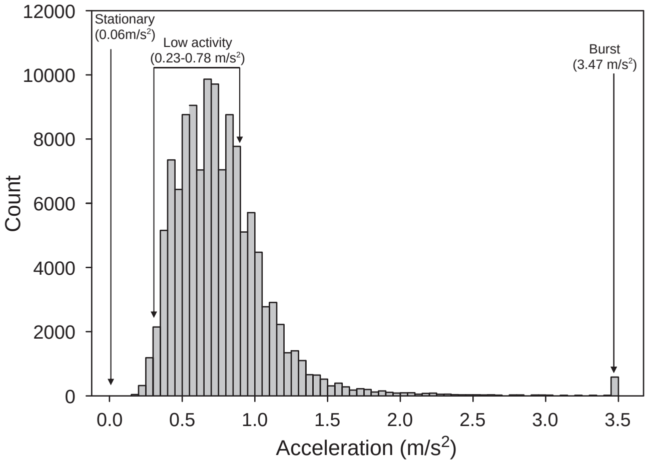

Fig. 3. Histogram of acceleration activity from free-swimming bonefish in the wetland mesocosm. Values for stationary, low activity, and bursting from laboratory calibrations were overlaid on the histogram for reference.

3.47 ± 0.00 m/s^2, respectively. Bursting activity exceeded the measurement capacity of the transmitter providing an effective endpoint for activity. A 'low activity' range was defined as the mean value for stationary alive bonefish minus the standard deviation up to the swimming bonefish plus the standard deviation (i.e., 0.23–0.78 m/s^2).

In the wild, five female and five male bonefish were implanted with acceleration transmitters (Table 1). Although the transmitters had an estimated battery life of 160 days, a number of fish were detected until the end of May/beginning of June 2009 (Table 1). Although bonefish #136 was detected until May 31, 2009, moving between 11 of the 13 receivers in the array, the acceleration data was consistently low (0.02 ± 0.02 m/s^2; mean ± SD) and less than that of a dead bonefish. As such, data for bonefish #136 were excluded from further analyses based on the assumption that the acceleration sensor had failed. A histogram was constructed for all acceleration data from the wild (Fig. 2). The mean acceleration value from free-swimming fish in the wild was 0.65 ± 0.43 m/s^2. The majority (76%) of acceleration values fell in the 'low activity' range (i.e., 0.23–0.78 m/s^2). Bursting activity was detected in the wild and made up 0.4% of all readings. Acceleration values did not differ between the sexes ($F = 3.453$, $p = 0.105$). There was no difference in daytime (0.69 ± 0.09 m/s^2; mean ± SE) or nighttime (0.61 ± 0.09 m/s^2; mean ± SE) acceleration values for wild bonefish ($F = 0.425$, $p = 0.524$).

A similarly shaped histogram was generated from bonefish acceleration data from the wetland (Fig. 3). The mean acceleration value for bonefish in the wetland was 0.78 ± 0.37 m/s^2. The majority (60%) of acceleration values fell in the 'low activity' range (i.e., 0.23–0.78 m/s^2), and bursting composed 0.5% of all readings. Nighttime acceleration values (0.87 ± 0.01 m/s^2; mean ± SE) were higher than daytime acceleration values (0.69 ± 0.01 m/s^2; mean ± SE) ($F = 70.428$, $p < 0.05$).

3.2. Ethogram study

Seven distinct behaviours were catalogued for bonefish in the wetland mesocosm (Table 3). The behaviours consisted of the following categories; stationary, swimming, drifting, bursting, flashing, nose dip, and face wedge (Table 2) (Fig. 4). Swimming accounted for the highest percentage (51.74%) of observed behaviour, followed by drifting (24.17%), and nose dip (16.96%) behaviours (Table 3). The observed bonefish tended to spend more time being stationary at mid-day, and more time bursting during pre-dusk hours (Table 2). More time was spent exhibiting nose dip and face wedge behaviours in the morning versus the other two time periods (Table 2). The average duration of most types of behaviour was less than 12 s, with only swimming behaviour lasting on average 16 s (Table 2). Because individual behaviours were short-lived combined with the nature of how acceleration values are recorded and transmitted, we were unable to assign distinct acceleration signatures to the observed behaviours.

3.3. Respirometry study

SMR was determined for 10 bonefish, while MMR_R was measured for seven. The three bonefish that were not measured for MMR_R would not adequately respond to exercise challenges and therefore were not subjected to further experimentation to avoid misrepresentation of data. The lowest recorded SMR was 59.6 mg O_2 kg^{-1} h^{-1}, and the highest SMR was 209.1 mg O_2 kg^{-1} h^{-1}. MMR_R ranged from 234.3 to 362.5 mg O_2 kg^{-1} h^{-1} (Table 3). By pairing laboratory-derived resting and bursting bonefish values with SMR and MMR_R, an equation of the line relating the two variables together was generated. The equation of the line is: oxygen consumption = 117.382 + 49.779 * acceleration ($r^2 = 0.745$, $F = 35.019$, $p < 0.0001$). With a mean acceleration of 0.65 m/s^2 for free-swimming bonefish in the wild, mean oxygen consumption is estimated as 149.7 mg O_2 kg^{-1} h^{-1} at 20.6 °C. As such, bonefish, on average, were only using 51.6% of their available estimated metabolic scope (i.e., 149.7 mg O_2 kg^{-1} h^{-1}/290.1 mg O_2

Table 2
Summary of the behaviours exhibited by bonefish in the wetland mesocosm, and the total duration, in seconds, that each behaviour was observed during morning, noon, and pre-dusk monitoring periods. Note each observation period was 10 min, and there were 20 observation periods at each time of day. The average duration ± SD of individual behaviours exhibited by bonefish in the wetland mesocosm are also indicated.

Behaviour	Description	Morning (7:10–9:20)	Mid-day (11:33–13:13)	Pre-dusk (17:11–18:52)	Total duration (s) and percentage (%) of total observed behaviour	Average duration ± SD (s) of behaviour
Stationary	Not moving horizontally	556	807	446	1809 (5.03%)	11.7 ± 8.7
Swimming	Steady horizontal movement while moving the caudal fin	5990	6193	6444	18 627 (51.74%)	16.4 ± 12.3
Drifting	Gliding through the water without movement of the caudal fin	2914	2979	2807	8700 (24.17%)	11.01 ± 6.2
Bursting	Fast horizontal swim, short duration	83	95	261	439 (1.22%)	8.0 ± 3.9
Flashing	Rolls onto side, get a flash of silver as the sun reflects off of the scales, returns to horizontal position	39	68	95	202 (0.56%)	7.5 ± 4.3
Nose dip	Nose of the fish dips toward the substrate	2326	1849	1930	6105 (16.96%)	11.1 ± 7.5
Face wedge	Face of the bonefish is wedged into the substrate	92	9	17	118 (0.33%)	9.1 ± 4.1
				Total	36 000 (100%)	

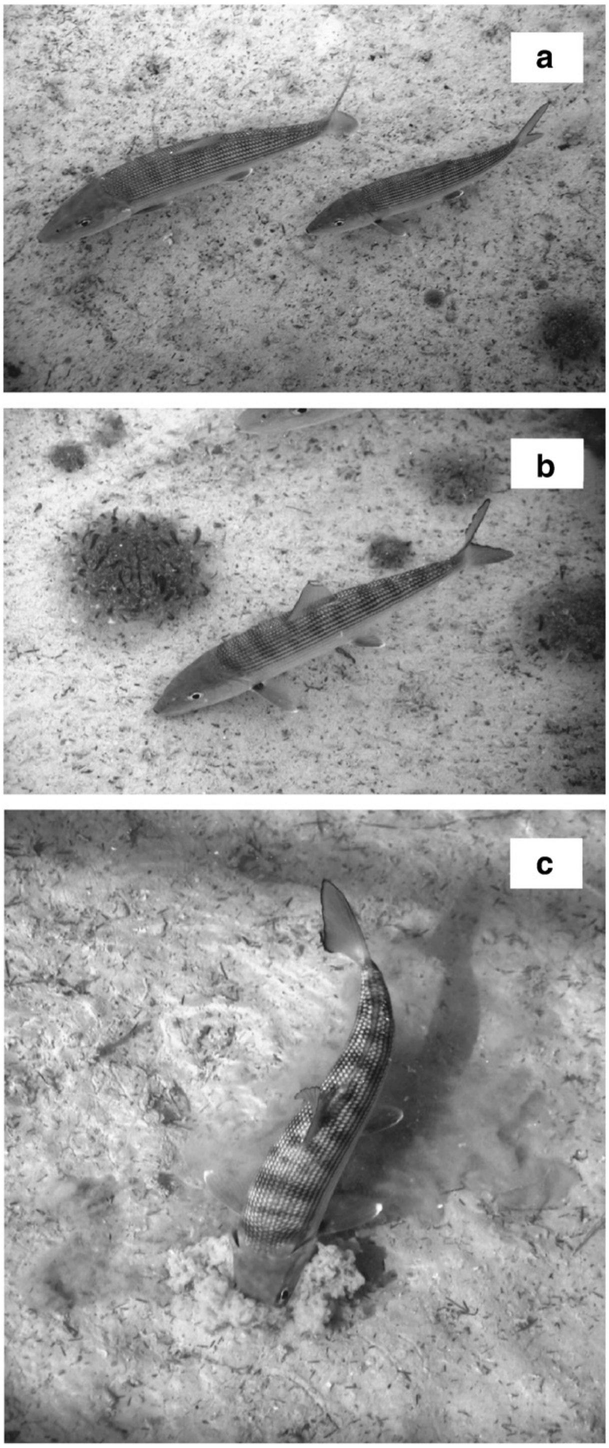

Fig. 4. Photographs demonstrating a) swimming behaviour (and schooling); b) nose dip behaviour; and, c) face wedge behaviour of bonefish held in a large wetland mesocosm. See Table 3 for a description of each behaviour.

$kg^{-1}\ h^{-1}*100$). The percentage of available estimated metabolic scope varied somewhat between individuals, but most fish used between 40 and 60% of their estimated scope the majority of time (Fig. 5). However, 0.7% of all observations exceeded 90% of estimated metabolic scope.

Table 3
SMR, MMR_R, and estimated metabolic scope for laboratory-acclimated bonefish at 20.6 ± 1.4 °C. SMR was calculated as the average of six lowest values recorded between 20:00 and 06:00. MMR_R was determined as the highest value recorded over a six hour recovery period after 4 min of exhaustive exercise. The estimated metabolic scope was calculated as the difference between the SMR and MMR_R. Three fish did not exercise after SMR trials so MMR_R, and thus scope could not be determined.

Total length (mm)	Weight (g)	SMR ($mg\ O_2\ kg^{-1}\ h^{-1}$)	MMR_R ($mg\ O_2\ kg^{-1}\ h^{-1}$)	Metabolic scope ($mg\ O_2\ kg^{-1}\ h^{-1}$)
458	810	59.6	234.3	174.8
416	932	117.2	247.2	130.1
430	802	118.0	277.5	159.5
404	508	100.6	280.7	180.1
417	887	186.6	295.3	108.7
330	420	209.1	333.3	124.2
340	348	159.5	362.5	203.0
393	590	135.3		
432	897	161.5		
445	679	74.4		

4. Discussion

This study represents the first attempt to quantify the field activity patterns of free-swimming bonefish in the wild using acoustic tri-axial acceleration transmitters. Because this is one of the few studies that have used acceleration transmitters rather than archival data logger for examining behaviour of wild fish, it is worth contrasting the two types of electronic tags (Table 4). There are some clear disadvantages to using acceleration transmitters rather than data loggers. In particular, with the transmitters used in this study, data are averaged across multiple vectors (3-axes) and over a 25 second sampling time. Given that most bursting activity lasts on the order of seconds, it is not surprising that most of the acceleration data collected consisted of low values. Nonetheless, many fish did 'max out' the device in the wild on numerous occasions. The fact that the transmitter reached measurement capacity at bursting is also a limitation in this study, as it is unknown if acceleration values at maximum swimming speeds are actually greater than 3.47 m/s^2 for bonefish. However, this can be remedied in the future by providing the manufacturer with user-defined acceleration ranges. Another constraint with the acceleration transmitter is the proportion of time the transmitter is actually sampling. With the transmitters used in this study, data was recorded for 25 s out of an average period of 180 s, thus only measuring acceleration approximately 15% of the time. While the delay time could be reduced to increase the proportion of time that acceleration is measured, such changes reduce the overall battery life of the transmitter. Acceleration data loggers on the other hand allow researchers to collect data on multiple axes at once and detect swimming activity from body undulations; however, loggers must be retrieved to access data and intense sampling frequency can lead to rapid battery depletion (e.g., days as opposed to months with the transmitter). Clearly there is a tradeoff here of which researchers must be aware. Transmitters last longer and data can be received remotely, but the data are not of high resolution. However, in the absence of any fine-scale data on the activity patterns of bonefish, data collected through the use of acceleration transmitters did provide considerable insights. The smallest available archival logger with tri-axial accelerometry sensors are still too big for even the largest bonefish used in our study. Moreover, annually we tend to only recover a small number of animals that we have previously tagged making the use of archival loggers for bonefish an expensive proposition that may yield very little data.

As mentioned above, the majority of acceleration values for bonefish were low (i.e., between 0.23 and 0.78 m/s^2). While these results may have been influenced by the functional capacity of the transmitters (i.e., averaging over 25 second period), the field observations are supported by ethogram data from the wetland mesocosm which found bursting activity to represent only 1.22% of total observed behaviour. Using acoustic telemetry, Block et al. (1992) found that blue marlin (*Makaira nigicans*), while capable of high

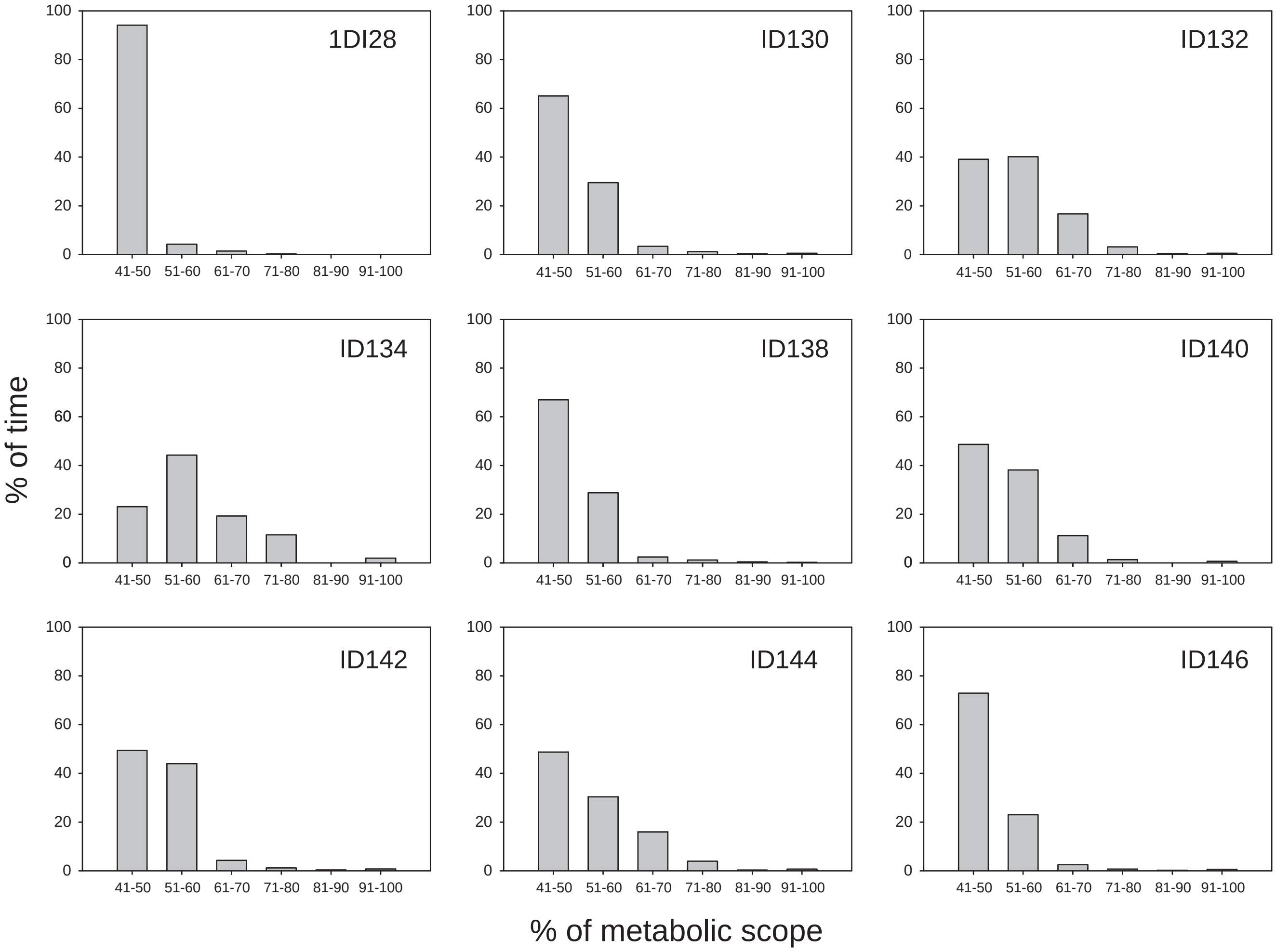

Fig. 5. Histograms of the percentage of time individual acceleration transmitter-implanted bonefish were at varying percentages of their metabolic scope in the wild.

swimming speeds, typically spent most of their time swimming slowly. Weihs (1984) suggested that the most energy-efficient swimming speed for a fish will be near the low end of their range. Even choosing an intermittent swimming style such as bursting-and-drifting can be energetically advantageous over constant swimming provided that the fish does not ram ventilate (Videler and Weihs, 1982). Indeed, bonefish in the wetland commonly followed up bursting or swimming behaviours with drifting. It is likely this activity pattern also contributed to lower acceleration values observed for bonefish in the wild.

Energetic efficiency plays a role in natural selection, and it has been suggested that a relationship between activity level and mortality may be the basis of that mechanism (Priede, 1977). Because animals need to operate within their scope for activity (Fry, 1947), any time they function at the limits of these bounds, their probability of death increases (Priede, 1977). As such, fish working at moderate power outputs are assumed to have a low probability of mortality due to natural causes (Priede, 1977). Transmitter-implanted bonefish in the wild tended to spend the majority of their time operating at between 40 and 60% of their estimated metabolic scope. Although there clearly are some limitations with how we related acceleration values to oxygen consumption (i.e., assumed a linear relationship between the two variables), we feel that this is a reasonable approach given the linear relationship between metabolism and acceleration documented in cormorants (Wilson et al., 2006), and the linear relationship between oxygen consumption and heart rate documented in fish studies (Priede, 1983; Lucas et al., 1991). We also acknowledge that we have not determined a true maximum metabolic rate since the transmitter not only reached their limit when we observed maximum metabolic rate (i.e., during chasing), but also because bursting is not aerobic, our estimates likely incorporate some element of anaerobic costs not measured here as well as the excess post-exercise oxygen consumption (see Lee et al., 2003). A future study should simultaneously measure acceleration and oxygen consumption of bonefish under controlled conditions in a swim flume equipped with respirometry apparatus to more accurately define the relationship between acceleration and metabolic rate, and the true metabolic scope for activity could be determined.

The lack of difference in activity level between day and night from both our ethology and field acceleration data was not surprising as bonefish movement patterns are more often associated with tidal cycles (Colton and Alevizon, 1983b; Humston et al., 2005; Murchie, 2010), and semi-diurnal tides occurred in the study area. No sex-related differences in activity patterns were observed through the use of acceleration transmitters. No differences in movement patterns between the sexes were observed using long-term positional telemetry on bonefish in the study area (Murchie, 2010). However, future studies should investigate potential difference in activity patterns of the sexes in offshore locations where bonefish are hypothesized to spawn during winter months (see Danylchuk et al., 2008).

Given that the timing of this study coincided with the hypothesized spawning period of bonefish, it is possible that some of the tagged individuals that were not detected beyond a week after release may have relocated to spawning habitats, or were moving in areas just outside of the hydrophone array. Previous studies on bonefish conducted in the study area revealed that the surgical procedures

Table 4
A comparison of the utility of acceleration data loggers versus acceleration transmitters. Note that for both loggers and transmitters it is possible to adjust device settings. We have attempted to generalize with approximate comparisons between the daily diary device (Wilson et al., 2007) and the Vemco V9AP-2L used in the current study.

Comparison of	Logger	Transmitter
Sampling frequency for acceleration	Often between 5 and 32 Hz (with variable rates specified for different channels).	Currently samples at 5 Hz but averages over user-determined period (25 s in this study).
Data retrieval	Data can only be retrieved when devices are recovered which may not be possible for free-swimming fish, particularly in open systems. Pop-off technology may be employed with the loggers to aid in retrieval.	Data can be transmitted remotely so animals do not need to be recaptured. However, data is only collected when fish is in the range of a hydrophone.
Number of channels	Loggers can typically record data from multiple sensors on different channels simultaneously and store it until analysis. That means that for acceleration data one can record all axes at once as well as data on water temperature, depth, orientation, etc.	Although data can be recorded on multiple channels, some on board processing is required as not all data can be transmitted simultaneously. In the case of the device used in this study, all three axes of acceleration were integrated into a single metric, thus reducing resolution. Additional sensors (e.g., depth or temperature) can be added but that reduces the time that will be devoted to recording and transmitting data on acceleration.
Potential to correlate with metabolic rate	Given that it is possible to detect tail beats from tri-axial accelerometry data, it is possible to establish relationships between tail beats and oxygen consumption.	Potential to correlate with metabolic rate more limited due to the averaging of the transmitter and inability to specifically quantify tail beats. Note that it is possible to only record one or two axes.
Commercial availability	Available for some.	Yes.
Longevity and size of device	The majority of acceleration loggers that would work on a large fish (approximately 5 kg or larger) without burdening the animal would only last for 1 day assuming that resolution is set to record multiple channels at 8 Hz.	Because of the reduced resolution in sampling time and the number of channels recorded, the devices can last >150 days.

followed in this study resulted in the continuous tracking of a number of individuals beyond six months and even up to two years (Murchie, 2010). Although it is not possible to know with certainty the fate of the animals, it is also possible that post-release predation may have occurred despite our attempts to provide extended recovery times, to optimize surgical procedures, and to minimize stress.

To our knowledge this was the first attempt to catalogue the discrete behaviours typically employed by bonefish. While observations on individuals occurred in a mesocosm environment, we believe these observations likely encompassed many of the behaviours exhibited by bonefish in the wild. When conducting an ethogram it is important not to infer the function of the behaviour as it could be misleading or potentially bias the observer (Martin and Bateson, 1993). After completing the observations however, it can be suggested that swimming, drifting, and bursting are clearly linked to locomotion, while 'nose dip' and 'face wedge' behaviours are associated specifically with food acquisition. The purpose of flashing behaviour is likely a comfort movement related to body care (Colgan, 1993). Ethograms provide a tool for future comparative studies (e.g., Müller et al., 1998), and are particularly worthwhile when considering costs and benefits of specific behaviours (Grantner and Taborsky, 1998). Future work with either refined acceleration transmitters, or even the use of acceleration archival data loggers, may reveal more details about fish behaviour in the wild (see Sakamoto et al., 2009 for ethograms generated from acceleration data from free-ranging birds).

In general, the information gathered on the behaviour and activity patterns of bonefish provides an effective starting point for the generation of a bioenergetics model for *A. vulpes*, particularly since no efforts have been made to date to generate metabolic data for this species. Production of a bioenergetics model for bonefish would not only provide fisheries managers with a useful tool for understanding bonefish production (Hansen et al., 1993) but would further assist scientists in understanding sub-tropical coastal ecosystem dynamics. Acceleration transmitters have a role in the ecologist's toolbox for elucidating activity patterns for fish that are not easily monitored, but researchers must understand their limitations prior to conducting studies.

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