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BEHAVIORAL ECOLOGY –ORIGINAL RESEARCH

Spatiotemporal drivers of energy expenditure in a coastal marine fish

Jacob W. Brownscombe[1] · Steven J. Cooke[1] · Andy J. Danylchuk[2]

Abstract Animal behavior and energy expenditure often vary significantly across the landscape, and quantifying energy expenditure over space and time provides mechanistic insight into ecological dynamics. Yet, spatiotemporal variability in energy expenditure has rarely been explored in fully aquatic species such as fish. Our objective was to quantify spatially explicit energy expenditure for a tropical marine teleost fish, bonefish (*Albula vulpes*), to examine how bonefish energetics vary across landscape features and temporal factors. Using a swim tunnel respirometer, we calibrated acoustic accelerometer transmitters implanted in bonefish to estimate their metabolic rates and energy expenditure, and applied this technology in situ using a fine-scale telemetry system on a heterogeneous reef flat in Puerto Rico. Bonefish energy expenditure varied most among habitats, with significant interactions between habitat and temporal factors (i.e., diel period, tide state, season). The energy expenditure was generally highest in shallow water habitats (i.e., seagrass and reef crest). Variation in activity levels was the main driver of these differences in energy expenditure, which in shallow, nearshore habitats is likely related to foraging. Bonefish moderate energy expenditure across seasonal fluctuations in temperature, by selectively using shallow nearshore habitats at moderate water temperatures that correspond with their scope for activity. Quantifying how animals expend energy in association with environmental and ecological factors can provide important insight into behavioral ecology, with implications for bioenergetics models.

Keywords Bioenergetics · Animal behavior · Landscape ecology · Acoustic telemetry · Acceleration transmitter

Introduction

Energy is considered the fire of life, acquired by organisms by consumption and expended for metabolic maintenance, activity, growth, and reproduction (Kleiber 1975; Tytler and Calow 1985). It is a key currency by which we can measure individual fitness, as well as population and ecosystem dynamics (Brown et al. 2004). Ultimately, organisms must acquire energy at a greater rate than it is expended to allocate resources to growth and reproduction; yet, tradeoffs must be made among various fitness-enhancing activities. For example, time and energy spent on predator avoidance often come at the expense of foraging (Milinski and Heller 1978; Hugie and Dill 1994; Lind and Cresswell 2005). Animal energetics may also vary due to spatiotemporal factors such as the distribution of resources, costs of movement, temperature, intraspecific competition, and predation risk (Lima and Dill 1990; Johnson et al. 1992; Lima and Zollner 1996; Hall and Clark 2016). The field of ecological energetics seeks to understand how ecological factors influence animal bioenergetics, with implications for fundamental ecology and predicting the impacts of anthropogenic stressors (Tomlinson et al. 2014).

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Bioenergetics models play a key role in understanding how animals make a living and allocate resources (Kleiber 1975; Harfmart and Brandt 1995). Active metabolism (i.e., energy used for movement) often constitutes a significant portion of energy budgets (Boisclair and Leggett 1989; Boisclair and Sirois 1993), but can be highly variable in the wild due to the influence of ecological factors on animal behavior and the energy expenditure (Houston et al. 1993; Brown et al. 2004; Shepard et al. 2013). Despite the fact that bioenergetics models are the most widely developed and applied in fish of any taxa (e.g., Hansen et al. 1993; Harfmart and Brandt 1995), variation in energy dynamics due to ecological factors in the wild are rarely integrated into estimates of metabolism (but see Payne et al. 2011; Brodie et al. 2016). Most empirical studies on wild fish bioenergetics either study fish in the laboratory or examine fish movement in relation to ecological factors (e.g., temperature), using growth or reproductive output as end points (e.g., Pauly 1980; Jobling 1995; Wurtsbaugh and Neverman 1988). Yet, energy expenditure is ultimately dependent on fish behavior and environmental conditions. For example, fish often behaviorally thermoregulate (Holland et al. 1992) or use specific water flows to minimize energy expenditure (Taylor et al. 2014; McElroy et al. 2012). With recent advances in biotelemetry and biologging technology, we can now acquire more direct estimates of energy expenditure, and potentially even energy gain (Cooke et al. 2016). This enables opportunities to quantify how fish expend energy in relation to ecological factors, providing greater insight into their spatial ecology, population dynamics, and improved estimates for bioenergetics models.

Here, we examine how ecological factors influence the energy expenditure of a benthivorous marine teleost fish, bonefish (*Albula vulpes*). Bonefish are a group of fishes that occupy shallow tropical and subtropical seas worldwide in diverse habitats including seagrass, sand, mud, and marl flats, and coral reefs, moving frequently between deepwater habitats into shallow nearshore areas with the tides (Humston et al. 2005; Danylchuk et al. 2011; Murchie et al. 2013). We used a swim tunnel respirometer to calibrate acoustic accelerometer transmitters to estimate energy expenditure with bonefish, and applied this technology to quantify energy expenditure with a fine-scale positioning system on a heterogeneous reef flat in Culebra, Puerto Rico. In doing so, we aimed to provide some of the most extensive estimates of the influence of ecological factors on energy expenditure of a teleost fish in the wild.

Methods

Accelerometer calibration

To estimate bonefish energy expenditure in the wild, we used acoustic accelerometer pressure transmitters (V13AP, 12.2 g in air, 35 s transmission delay, ±3.43 g acceleration range, 5 Hz sampling frequency; Vemco, Bedford, Nova Scotia). These transmitters function by measuring acceleration (g, 9.8 m s^2) in three axes (x = lateral, y = forward, and z = vertical) and processing the information before transmission. The root mean square (RMS) of acceleration (a) is calculated as: $a = \sqrt{A_x^2 + A_y^2 + A_z^2}$, where A represents acceleration in each axis. The RMS is averaged over each sampling period (25 s) and stored in memory until transmission.

We calibrated accelerometer transmitters to predict mass-specific oxygen consumption rate (MO$_2$; O$_2$ min^{-1} kg^{-1}) in bonefish using a Blazka-style flowthrough respirometer swim tunnel at the Cape Eleuthera Institute (CEI) in Eleuthera, the Bahamas, using a two-step experimental approach, by first calibrating acceleration with swimming speed and then swimming speed to MO$_2$. It is well established that the dynamic acceleration generated by animals is highly correlated with the rate of movement and metabolism in a wide range of species from diverse taxa (Halsey et al. 2011), including fish (Gleiss et al. 2010; Wilson et al. 2013; Wright et al. 2014). Firstly, we determined the relationship between transmitter-derived acceleration and bonefish swimming speed. Bonefish (n = 10; 42 ± 6 cm fork length; mean ± SD; range = 32–53 cm) were captured from a tidal mangrove creek in Eleuthera via seine net on 10 January 2014 and transported back to a wet laboratory facility at CEI (as per the methods in Murchie et al. 2009). Fish were held in a large circular tank (3.7 m diameter × 1.25 m height; 13,180 l) for 3–7 days prior to experimentation and were fed daily rations of cut fish to satiation.

Prior to experimentation, bonefish were tagged with V13AP transmitters. Bonefish were anesthetized with 100 ppm tricaine methanesulfonate (MS-222), placed dorsal side down on a surgery table and supplied with recirculating seawater containing a maintenance dose of 50 ppm MS-222 (as per Murchie et al. 2011). A 2–3 cm incision was made with a scalpel ~2 cm from the ventral midline of the fish posterior to the pectoral fins, and transmitters were implanted into the coelomic cavity with the sensors facing anteriorly. The incision was closed with two to three interrupted sutures using absorbable monofilament suture

materials (Ethicon 3-0 PDS II, Johnson and Johnson, New Jersey). Twenty-four hours after surgery, bonefish were placed in a Blazka-style swim tunnel (24.1 internal diameter × 116 cm length; see Thorstad et al. 1997 for additional details) and given 1 h prior to the swimming protocol to acclimate to the tunnel. Water flow was increased to 10 cm/s until the bonefish maintained its position in the tunnel (swimming the same speed as the flow) for at least three successful data transmissions. Swimming speeds were increased by 15 cm/s thereafter following the same protocol. The flow speed was increased until the fish could no longer maintain its position in the tunnel, i.e., when its tail was touching the back grate for >5 s. Bonefish were then transferred to a holding tank to recover for 24 h, when transmitters were surgically removed. Bonefish were held for another 24 h for recovery and released back into the wild.

The experiments conducted to estimate the relationship between bonefish swimming speed and MO_2 were reported in Nowell et al. (2015). Briefly, bonefish ($n = 66$; 41 ± 4 cm fork length; 847 ± 257 g; mean $\pm$ SD; range = 34–51 cm) were subjected to a ramp-Ucrit procedure (Jain et al. 1997) involving 15 cm/s increases in swimming speed every 15 min until exhaustion. Oxygen consumption was measured at each speed over a 10 min period with an OxyGuard oxygen probe (OxyGuard Handy Polaris 2, portable DO meter, Water Management Technologies, Inc. Baton Rouge, LA, USA). Swimming trials were run from October 2012 to November 2013 to collect metabolic estimates from a range of temperatures bonefish experience in the wild, 22–36 °C, with a range of sizes at each temperature (Nowell et al. 2015).

Study site and habitat mapping

The field study was conducted in Culebra, Puerto Rico, on a fringing coral reef flat named Las Pelas (18.2966°N, −65.2500°W). To characterize habitats in the study area, depth, and abiotic and biotic conditions were quantified at 487 locations along four transects spanning beyond estimated bonefish locations in all directions (See Supplementary Material, Fig. 1 for locations). At each location, the percentage benthic cover of substrate (sand, coral rubble, or sand/fine sediment), seagrass (*Thalassia testudinum, Syrungodium filliforme, Halodule wrightii*), macroalgae (*Halimeda* spp., *Penicillus* spp), and coral (dead hard coral, live hard coral, or live soft coral, *Diploria, Millepora, Gorgoniidae*) were visually estimated within a 1-m² quadrat. Using these samples, five distinct habitat types were identified with a k-means clustering algorithms to minimize the sum of squares (Supplementary Material, Fig. 2). These included *forereef*—mainly live and dead hard corals and coral rubble, *reef crest*—primarily coral rubble and sand,
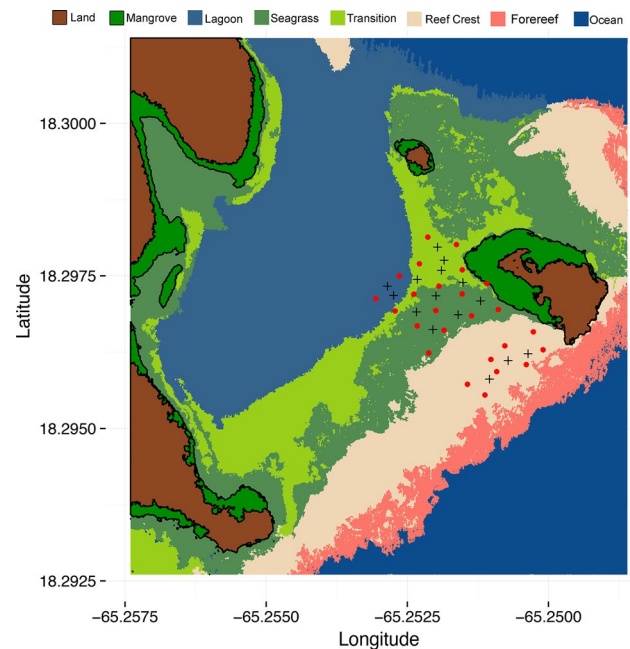

Fig. 1 Las Pelas fringing reef in Culebra, Puerto Rico. *Colors* represent habitat types identified using a k-means clustering algorithm based on habitat samples and predicted across the entire area using a maximum likelihood classification algorithm on satellite imagery. *Red circles* represent acoustic receiver locations and *black crosses* synchronization tags, comprising the Vemco Positioning System (color figure online)

seagrass—seagrass with sparse macroalgae and sand, *transition*—mainly sand with some macroalgae and seagrass, and *lagoon*—sand/soft sediment with sparse macroalgae (Fig. 1; Supplementary Material, Table 1). The spatial distribution of each habitat type was then estimated throughout the study area using a semi-automatic classification algorithm on satellite imagery of the study region with known habitat types from sampling locations as training reference points using the program QGIS Version 2 (Quantum GIS 1991).

Depth was measured at a subset ($n = 107$) of the habitat sampling locations using a Hawkeye D10 Depth Sounder (NorCross Marine Products, Inc, USA) for locations >1 m in depth, or a measuring tape at locations <1 m. Time was also recorded to correct for tide height at the time of sampling. Depths were estimated throughout the study region using kriging interpolation. The mean depth in the lagoon was 4.83 m, transition 1.40 m, seagrass 0.73 m, reef crest 0.70 m, and coral reef 2.65 m.

Acoustic tracking system and fish tagging

To quantify spatially explicit bonefish energy expenditure on Las Pelas, a fine-scale acoustic telemetry array (Vemco Positioning System, VPS) was deployed in August 2012, consisting of 25 VR2 W receivers (69 kHz, Vemco) and 15

acoustic transmitter synchronization tags (Vemco V13-1x, 500–700 transmission delay) (Fig. 1). Synchronization tags were used to maintain time synchronization in the tracking system, as well as provide estimates of positioning error from known locations. Based on initial range tests indicating low detection range in this shallow, noisy system, receivers were spaced apart by 50 m to ensure overlapping detection ranges. The system was established to track bonefish, permit (*Trachinotus falcatus*), great barracuda (*Sphyraena barracuda*), and green sea turtles (*Chelonia mydas*) from August 2012 to December 2014. Based on preliminary observations of temperature differences between the forereef and backreef habitats, water temperature was measured once per hour in two locations, one on the forereef and the other on the transition habitat using temperature loggers (Hobo Pendant UA-002-64, Onset Computer Corp, Onset MA, USA).

The bonefish examined here ($n = 10$, 52.1 ± 6.1 cm, mean $\pm$ SD, 41–60 cm range) were tagged via surgical implantation in the coelomic cavity with Vemco acoustic accelerometer pressure transmitters (V13AP, 12.2 g, 45–135 s transmission delay, ± 3.43 g acceleration range, 323 day battery life, 5 Hz sampling frequency) from 27 April 2013 to 22 May 2013. Fish were captured by fly or spin fishing on the reef crest and seagrass habitats of Las Pelas. Upon capture, fish were held in a floating mesh net pen ($1.5 \times 1.5 \times 1.5$ m) for a minimum of 20 min prior to the tagging procedure. Acoustic transmitters were then surgically implanted in bonefish using the same methods as the swim tunnel experiment described above. Bonefish were held in the net pen for a minimum of 1 h prior to release due to concerns about post-release predation with this species (see Danylchuk et al. 2007; Brownscombe et al. 2013).

Data analysis

For the swim tunnel accelerometer transmitter experiment, bonefish acceleration was square root transformed and fit with a linear mixed effects (LME) model with swimming speed as a fixed effect and individual fish as a random effect. For the respiration swim tunnel data, bonefish MO_2 (mg O_2 min^{-1} kg^{-1}) was square root transformed and fit with an LME with swimming speed, fish fork length, temperature, and the interaction between swimming speed and temperature as fixed effects and individual fish as a random effect.

Detections of acoustically tagged bonefish by at least three acoustic receivers in the Vemco positioning system in Culebra were used by Vemco to estimate fish positions using hyperbolic positioning (Smith 2013). Estimated bonefish positions with associated acceleration data ($n = 52,921$) were filtered by a maximum horizontal positioning error

(HPE) of ten (Supplementary Material, Fig. 3), following the methods of Smith (2013), which retained 83% of detections. This error estimate is not spatially explicit, but in synchronization tags, applying this maximum HPE value filter resulted in a mean error of 1.2 ± 2.2 m SD. For each fish, the initial 24 h of data were also excluded from the data set. Retained acceleration values ($n = 42,350$) were used to estimate bonefish MO_2 using the two models described above. Temperature was derived from the spatially and temporally nearest environmental temperature logger to the fish. Bonefish MO_2 estimates were converted to energy expenditure (J min^{-1} kg^{-1}) assuming 1 mg O_2 equated to 14.1 J of energy expended, the standard for ammonotelic fishes (Elliott and Davison 1975). To examine how bonefish energy expenditure varied with ecological factors, 10,000 data points were randomly subsetted prior to modeling. These data were fit with a generalized least squares regression with log-transformed bonefish energy expenditure (J min^{-1} kg^{-1}) as the response variable and habitat, season, diel period, tide state, as well as habitat:season, habitat:diel period, and habitat:tide state interactions as predictors. To account for correlation within individuals, an autocorrelation structure was implemented with individual fish as a grouping factor and a continuous time covariate (Pinero and Bates 2000). A variance structure was also used to account for variance heterogeneity among habitat types. To determine if bonefish were using the reef flat selectively based on water temperature, temperatures where bonefish were present within the tracking system were compared to all measured temperatures during the study period using a generalized linear mixed effects model with a poisson link function, data type (fish, environment) as a predictor, and season nested in data type as a random effect.

All statistical analyses were conducted using RStudio version 0.99.473 (RStudio Team 2015) and R (R Core Team 2013). Models were fit using the R packages 'nlme' (Pinheiro et al. 2015) and 'lme4' (Bates et al. 2015). Model selection was conducted using the drop1 command to compare full models to reduced models with log ratio tests. Models were validated using the procedure outlined in Zuur et al. (2009).

Results

Accelerometer calibration

There was a significant positive relationship between accelerometer transmitter-derived bonefish acceleration (ACC) and swimming speed (SS) in the swim tunnel (Table 1; Fig. 2), described by Eq. 1:

$$SS = (\sqrt{ACC} - 0.57)/0.013. \qquad (1)$$

Table 1 Linear mixed effects model outputs for bonefish acceleration (measured with a V13AP transmitter) and metabolism (MO_2) measured in a swim tunnel respirometer.

Response variable factor	Coefficient	SE	DF	*t* value	*p* value
Acceleration					
Intercept	0.57	0.03	260	22.78	*<0.001*
Swim speed	0.01	0.00	260	43.06	*<0.001*
MO_2					
Intercept	1.16	0.72	231	1.61	0.11
Swim speed	0.03	0.01	231	3.00	*0.003*
Fork length	−0.02	0.01	63	−1.62	0.11
Temperature	0.05	0.02	63	3.09	*0.003*
Speed × temperature	0.0005	0.00	231	−1.32	0.19

Italics indicate significant predictors

With untagged bonefish, swimming speed, fork length (FL), water temperature (*T*), and the swimming speed × temperature interaction were all significant predictors of oxygen consumption in the swim tunnel (Table 1; Fig. 2), described by Eq. 2:

$$\sqrt{MO2} = 1.16 + 0.03 \times SS - 0.02 \times FL + 0.05 \times T$$
$$+ 0.0005 \times SS : T. \quad (2)$$

Spatial bioenergetics

The fine-scale spatial positioning system on Las Pelas provided 42,350 reliable positions with acceleration estimates from nine bonefish from 30-04-2013 to 20-03-2014. The overall estimated mean rate of energy expenditure by bonefish in the tracking system was 73 J min^{-1} kg^{-1}, (5.2 mg O_2 min^{-1} kg^{-1}). There was variability in bonefish energy expenditure across habitats and temporal factors, with significant interactions between temporal factors (diel period, tide state, season) and habitat (Table 2; Fig. 3). Across the aquatic landscape, bonefish expended more energy in shallower habitats, with the highest rates on the reef crest at night (Fig. 4a). Differences in energy expenditure among tides were less pronounced than across habitats, but energy expenditure was generally higher during high and ebbing tides (Fig. 4b). Energy expenditure was fairly consistent between seasons in deeper water habitats (i.e., lagoon and transition), but more variable by season on the seagrass and reef crest, and consistently lower in the winter than other seasons (Fig. 4c).

Due to the nature of the predictive models developed in the swim tunnel experiments, water temperature and acceleration were intrinsically related to the estimates of bonefish energy expenditure. However, examining the factors that contributed to energy expenditure in the wild, activity (acceleration) had a greater influence over energy expenditure than temperature due to the relatively narrow range of temperatures experienced (Fig. 5a). Bonefish activity levels increased with
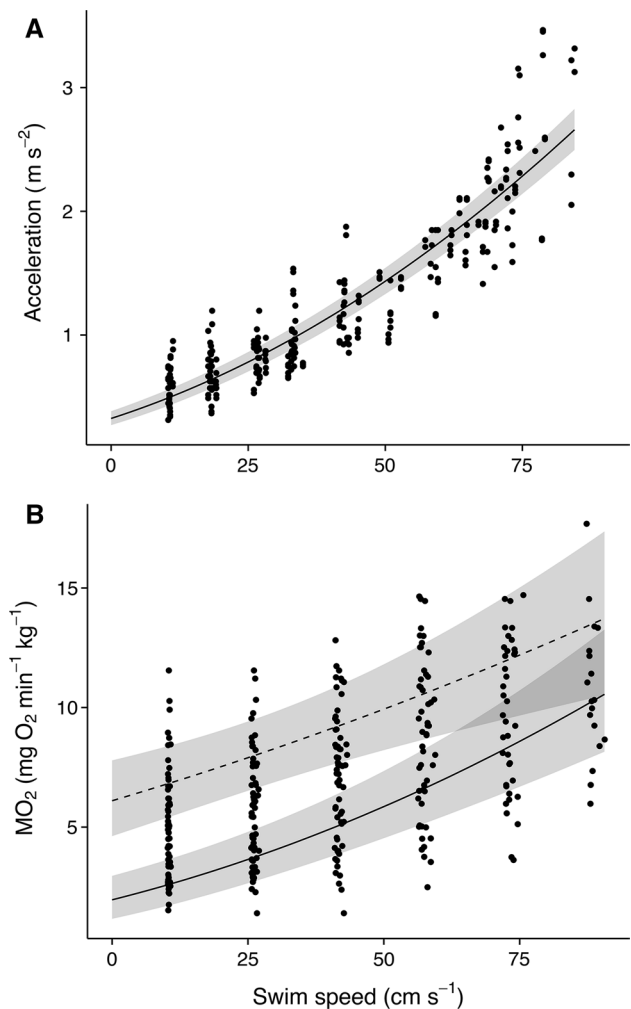
Fig. 2 a Bonefish (*n* = 10) swimming speed (m s^{-1}) and acceleration (m s^{-2}) in a swim tunnel measured with V13AP transmitters and fitted linear mixed effects model predictions ±95% CI. **b** Bonefish (*n* = 66) swimming speed (m s^{-1}) and metabolic rate (MO_2; mg O_2 min^{-1} kg^{-1}) and linear mixed effect model predictions for a 61 cm fork length bonefish at 22 °C (*solid line*), and a 34 cm fish at 36 °C (*hatched line*) ±95% CIs, as examples to illustrate the effects of fish size and water temperature on bonefish metabolism

temperature, but declined above 30 °C (Fig. 5b). Water temperatures were also significantly different when bonefish were present in the area than the temperatures available (GLMM; *z* = 4.73, *p* < 0.001). During the winter and spring seasons, bonefish occupied the study area selectively when water temperatures were warmer, while in summer and fall seasons, bonefish were selected for colder temperatures (Fig. 6).

Discussion

The field of ecological energetics explores how ecological factors such as temperature, habitat, and prey distribution

Table 2 Significant predictors of bonefish energy expenditure ($J\ min^{-1}\ kg^{-1}$) estimated with generalized least squares regression

Predictor	df	F value	p value
Habitat	3	372.1	<0.001
Diel period	1	13.1	<0.001
Season	3	74.5	<0.001
Tide state	3	19.7	<0.001
Habitat:diel period	3	39	<0.001
Habitat:season	9	16.1	<0.001
Habitat:tide state	9	4.3	<0.001

Data are derived from accelerometer transmitters within a fine-scale positioning system on Las Pelas reef flat, Culebra, Puerto Rico
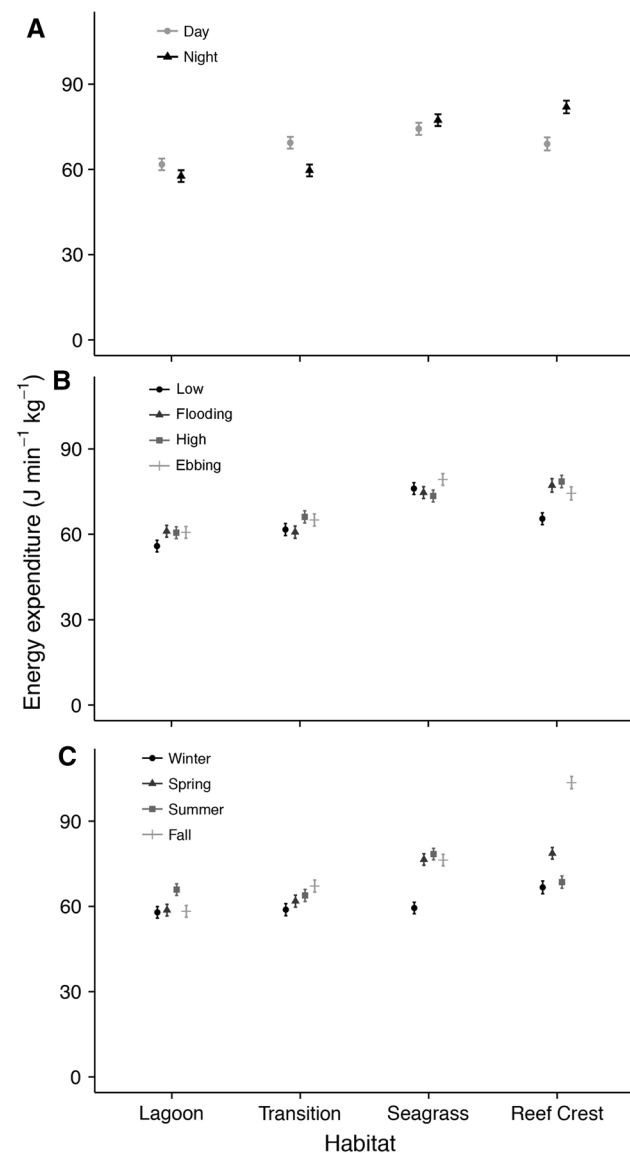
Fig. 3 Generalized least squares estimates ±95% CIs of bonefish energy expenditure ($J\ min^{-1}\ kg^{-1}$) by **a** habitat type and diel period, **b** habitat type and tide state, **c** habitat type and season
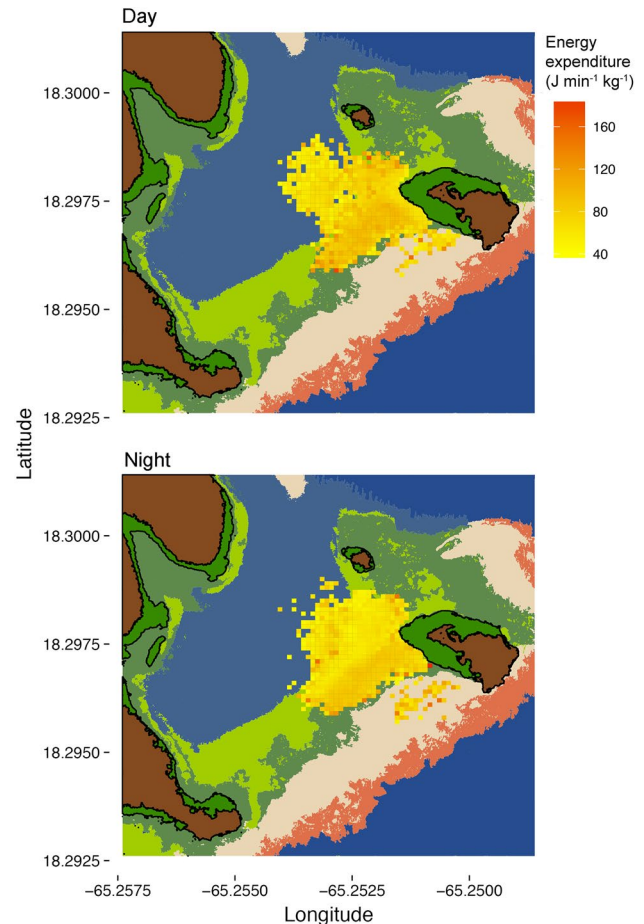
Fig. 4 Bonefish energy expenditure ($J\ min^{-1}\ kg^{-1}$) on Las Pelas reef flat

influence the energetics of animals, with implications for their spatial distributions, population dynamics, and responses to anthropogenic stressors (Tomlinson et al. 2014). To date, few studies have examined how ecological factors influence the energy dynamics in fully aquatic species such as fish. Here, we examined spatially explicit energy expenditure in a tropical marine fish, revealing the interactive effects of landscape features and temporal factors. Habitat was the strongest predictor of bonefish energy expenditure, increasing from the lowest in the deepwater lagoon, to the highest in the shallow water seagrass and reef crest. Given that the energy expenditure was driven mainly by variability in activity more than water temperature, these differences across habitats were a consequence of bonefish behavior. Shallow, nearshore habitats are believed to represent important foraging grounds for bonefish (Colton and Alevizon 1983; Humston et al. 2005; Murchie et al. 2013), although this has not been quantified directly in scientific studies. Animals often expend greater amounts of energy foraging, although this depends on the foraging mode (Huey and Pianka 1981; Anderson and Karasov
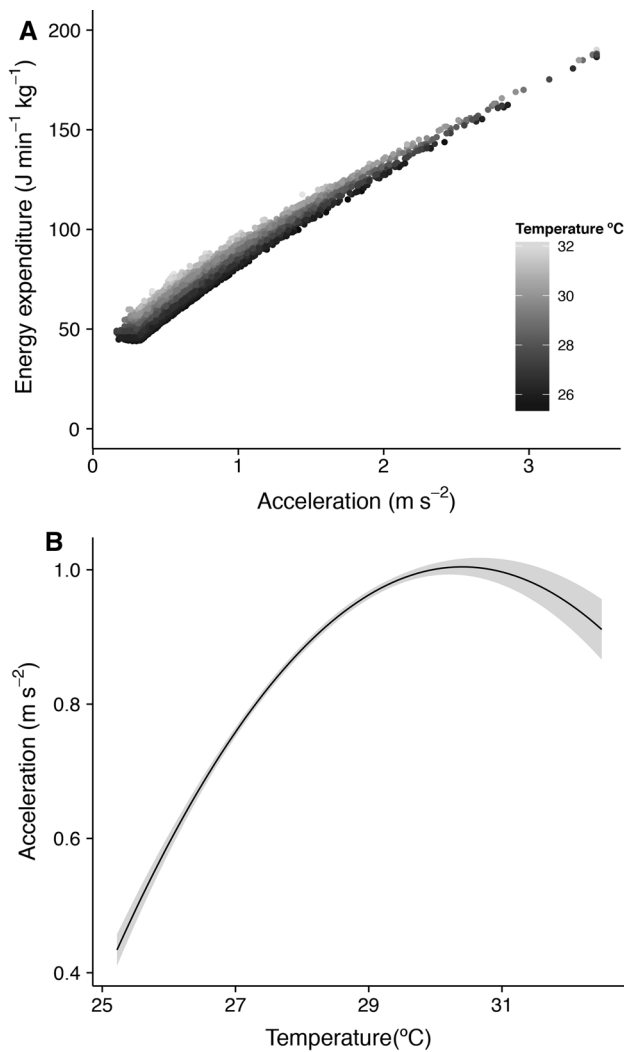
Fig. 5 a Bonefish acceleration (m s^{-2}) and energy expenditure (J min^{-1} kg^{-1}) across a range of water temperatures, **b** water temperature (°C) and bonefish activity (acceleration, m s^{-2})

1981; Arnould et al. 1996). Bonefish forage actively in the benthos, searching for and capturing diverse preys such as crabs, shrimp, and small fish (Colton and Alevizon 1983; Crabtree et al. 1998). Greater bonefish energy expenditure observed here in shallow water environments likely reflects foraging behavior, supporting previously anecdotal evidence of foraging locations, which in Culebra were primarily the seagrass and reef crest (coral rubble) habitats.

Landscape characteristics can have a profound effect on the energetic costs of movement (i.e., the energy landscape; Wilson et al. 2012; Shepard et al. 2013), which influences animal movement paths. Indeed, variability in water flow in river systems influences the movement activity of pallid sturgeon (*Scaphirhynchus albus*; McElroy et al. 2012) and also incurs energetic costs to Pacific salmon (*Oncorhynchus* spp.; Hinch and Rand 1998; Burnett et al. 2014). Rather

than examine movement paths, we explored how bonefish expend energy in relation to ecological factors including habitat type, diel period, and tidal state. While nearshore marine environments generally have less water flow than river systems, bonefish energy expenditure was higher during ebbing tides, which may be related to increased costs of remaining in shallow water habitats in flowing water. Given that habitat has a significant impact on animal behavior, which is paid for in energy (Tytler and Calow 1985), it is important to consider animal behavior and habitat function in quantifying spatially explicit energy dynamics. In this context, ecological factors such as the presence of predators or prey distribution may also generate significant variability in energy expenditure across space and time (Lima 1986; Milinski 1986; Houston et al. 1993; Hall and Clark 2016). By understanding the factors that contribute to animal energetics in the wild, we may gain insight into individual and population level characteristics such as growth. For example, ecological energetics may help explain why bonefish growth rates are significantly higher in Puerto Rico and Florida than the Bahamas (Crabtree et al. 1996; Adams et al. 2008).

Water temperature is a key driver of fish metabolism (Fry and Hart 1948; Brett 1964; Clarke and Johnston 1999), and also varied significantly across seasons in the study region. This was a contributing factor in seasonal variability in bonefish energy expenditure, which was generally lowest in the winter. However, bonefish also utilized this nearshore reef flat selectively at more moderate temperatures, avoiding the extreme lows in the winter and highs in the summer, moderating energy expenditure. Further, bonefish activity rates (acceleration) were also related to temperature, where activity peaked at 30 °C and declined sharply at higher temperatures. This is consistent with the findings of Nowell et al. (2015), which showed that critical swimming speed and scope for activity decline above 30 °C in this species. While bonefish locations were unknown when outside the range of the tracking system, bonefish in this environment have extremely high fidelity to certain reef flats (AJ Danylchuk, unpublished data) and were likely located in adjacent deeper water habitats where they frequent (Murchie et al. 2013). Water temperature is a strong driver of habitat selection in fish (Freitas et al. 2015) as they balance tradeoffs between energy acquisition, gain, and predation risk. Because nearshore habitats are important foraging habitats for bonefish, exclusion from these areas at warm temperatures may have impacts on their energetics during warmer months. Under climate change scenarios, increases in water temperature may cause greater exclusion from potentially important shallow, nearshore foraging habitats (Wenger et al. 2011).

Despite the important insights gained from quantifying energy expenditure in the wild, along with the fact that
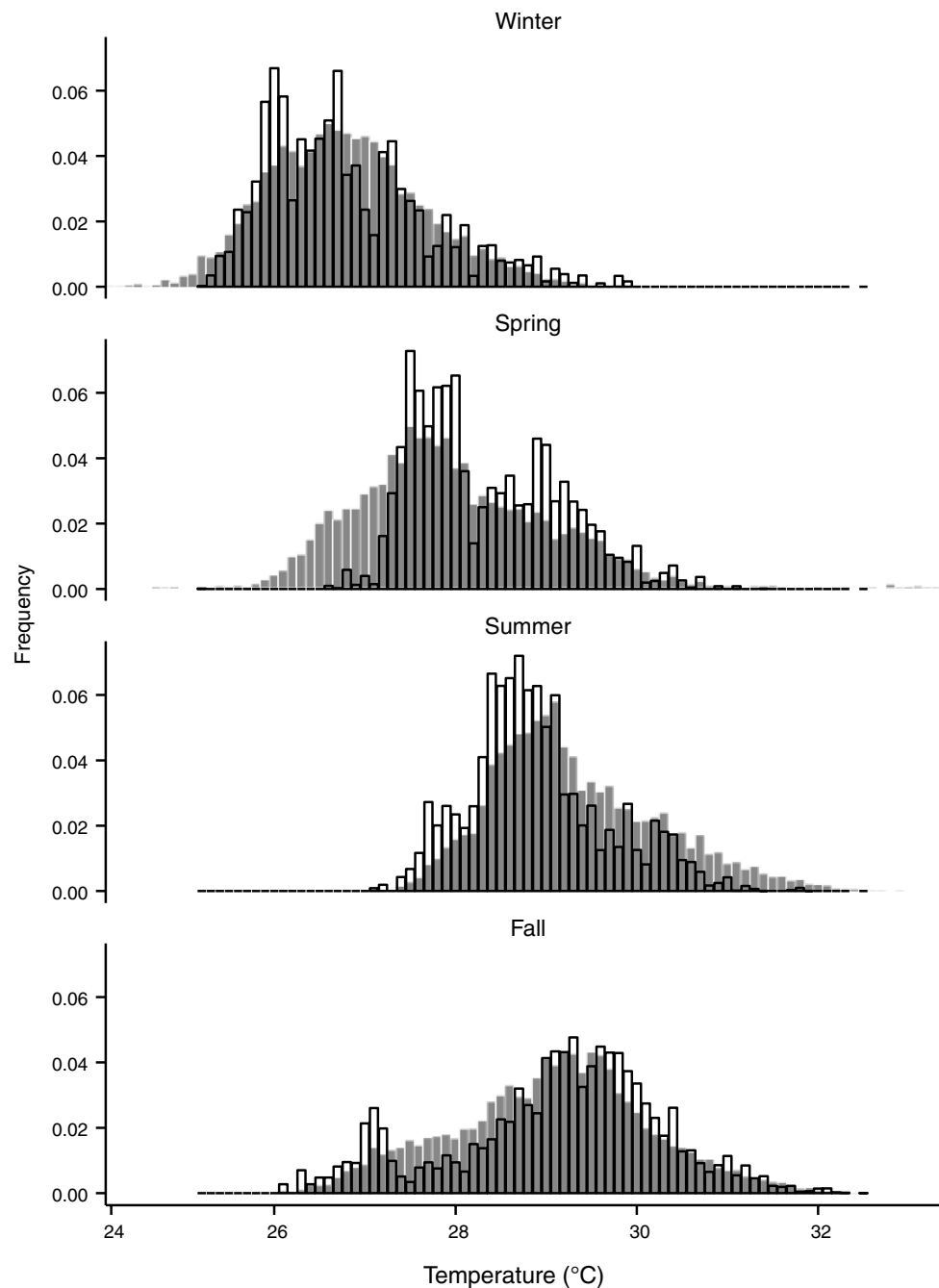
Fig. 6 Frequency of water temperatures in Las Pelas when tagged bonefish were present (*white bars*) and overall during the study period (*gray bars*)

bioenergetics models are the most widely developed and applied in teleost fishes (e.g., Hansen et al. 1993; Harfmart and Brandt 1995), this study is one of the first to explore how fish expend energy in relation to aquatic landscape characteristics by integrating both the costs of activity and the influence of water temperature. This is likely due to the challenges of quantifying energy expenditure and position simultaneously in fully aquatic species (Cooke et al.

2016). Global positioning systems do not function underwater; instead, we must rely on acoustic telemetry systems to quantify position, which typically provides a very coarse estimate of location, within ~50–1000 m of an acoustic receiver in three dimensions, while receivers rarely cover the entire area a fish uses, providing discontinuous data (Cooke et al. 2004). However, with recent advances in hyperbolic positioning we can now estimate fine-scale

fish positions (Espinoza et al. 2011). Further, tools for estimating energy expenditure (e.g., accelerometers or heart rate loggers calibrated to estimate oxygen consumption) are typically biologgers, meaning we must rely on recapture of the tagged animal to acquire the information (Clark et al. 2010a; Gleiss et al. 2010; Brown et al. 2013), which is challenging for the fish. To overcome this challenge, Payne et al. (2011) used a swim tunnel to calibrate accelerometer transmitters to estimate energy expenditure in Australian cuttlefish (*Sepia apama*) and estimated their metabolic rates in the field with acoustic receivers. Building on this approach, we expanded this calibration method to include the range of temperatures bonefish would experience in the wild, and tracked accelerometer-tagged bonefish using a fine-scale acoustic telemetry system. In doing so, we were able to generate spatially explicit, activity- and temperature-based estimates of bonefish energy expenditure over an 11-month period in the wild. One major limitation with this approach is that swim tunnels generate linear swimming only; the energetic costs of more complex maneuvers are not incorporated despite the fact that turning can be energetically costly (Boisclair and Leggett 1989). Accelerometer biologgers have shown promise for identifying more complex behaviors, including foraging in this species using tail beat activity and body posture data (Brownscombe et al. 2014), which can now be integrated into transmitter technology (de Almeida et al. 2013). While accelerometers can measure activity and behavior, another general limitation is that they cannot capture other sources of energy expenditure such as the costs of digestion, which heart rate loggers can measure (Clark et al. 2010b). As transmitter technology develops to incorporate more sensors, future studies may integrate more accurate measures of energy expenditure, as well as energy gain via foraging.

Here, we found that energy expenditure is associated with landscape features in a teleost fish in a nearshore tropical marine system, which was mainly due to habitat-specific fish behavior. While water temperature is a major factor affecting fish metabolism, bonefish moderated energy expenditure by avoiding nearshore areas during temperature extremes. Understanding how ecological factors influence fish energy expenditure may lead to greater insight into how they distribute themselves in space and time (Shepard et al. 2013), as well as develop more accurate bioenergetics models (Brodie et al. 2016). Further, quantifying ecological energetics may provide insight into individual and population-level dynamics such as growth rates and population sizes. This may be particularly useful for predicting how changing environmental constraints due to anthropogenic stressors such as climate change impact individuals and populations (Tomlinson et al. 2014). Aquatic ecosystem characteristics (e.g., temperature, current, dissolved oxygen) are extremely spatiotemporally variable, and associated energetic costs are a probable mechanism for the diversity in spatial ecology and population dynamics observed in fish and other aquatic species. As biotelemetry and biologging technology continues to advance (Hussey et al. 2015), future research may aim to explore ecological energetics in fish over greater temporal and spatial scales and associations with diverse biotic and abiotic factors to gain insight into their ecology.

Author contribution statement JWB designed the research project, conducted experiments and field studies, analyzed the data, and wrote the manuscript. AJD and SJC contributed to research design, manuscript preparation, and provided funding.

Compliance with ethical standards

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