Swimming energetics and thermal ecology of adult bonefish (*Albula vulpes*): a combined laboratory and field study in Eleuthera, The Bahamas

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Abstract Knowledge of the swimming energetics and thermal ecology of sub-tropical and tropical coastal species is extremely limited, yet this information is critical for understanding animal–environment relationships in the face of climate change. Using the ecologically and economically important sportfish, bonefish (*Albula vulpes*), we determined the critical swimming speed (U_{crit}), metabolic rates (MO_{2max} and $MO_{2routine}$), scope for activity, and cost of transport (COT_{net}) across a range of temperatures using a swim tunnel. For both critical swimming speed and scope for activity, optimal (T_{opt}) and critical (T_{crit}) temperatures were determined. The optimal temperature for U_{crit} (96 cm/s) was 28.0 °C and the optimal temperature for scope for activity (7.5 mgO$_2$/min/kg) was 26.7 °C. We also estimated the thermal profile of bonefish in the wild using surgically implanted thermal loggers. Of the 138 implanted fish, eight were recaptured with functional loggers. After 220 days more than 55 % of recaptured tagged fish had expelled their thermal loggers. Thermal profiles revealed that bonefish did not exceed laboratory-determined critical temperatures (i.e., 14.5 °C minima and 37.9 °C maxima) and spent the majority of their time at their critical swimming speed optimal temperature. Nonetheless, fish experienced wide variation in daily temperature—both through time (up to 8 °C diel fluctuation and 14 °C seasonally) and among individuals. Collectively, laboratory and field data suggest that bonefish occupy habitats that approach, but rarely exceed (0.51 % of the time) their T_{crit}. Bonefish routinely experienced water temperatures in the field that exceeded their T_{opt} (~54 % of the time). Even minor increases in temperature (e.g., 1 °C) in tidal creeks will lead to greater exceedances of T_{opt} and T_{crit} or potentially reduce access of bonefish to essential feeding areas.

Keywords Bonefish · Swimming · Respirometry · Temperature · Biologger · Scope for activity

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Introduction

Water temperature is considered the "master" environmental factor influencing the biology of fish because it influences all biochemical, physiological, and life

history activities (Brett 1971). Information on the thermal biology of fish provides insights into their distribution, habitat use and bioenergetics, ultimately driving growth, foraging, predator escape and reproductive investment (Clark et al. 2013). Temperature is dynamic, changing on a diel and seasonal basis, influencing ecological dynamics and imposing challenges to organisms. In tropical oceans, temperatures are expected to be 2.0 °C higher by the 2050s and 3.0 °C higher by the 2080s, relative to a 1990 baseline (Nurse 2011). Tropical and sub-tropical regions, such as the Caribbean Sea and The Bahamas, have characteristics that make them uniquely vulnerable to the anticipated effects of climate change (Stocker et al. 2013). One of these key characteristics is their geographic vulnerability, especially as the Caribbean includes vast coastal flats ecosystems. These coastal flats ecosystems are expanses of shallow nearshore environments, which include a diverse mosaic of habitats such as seagrass beds, tidal mangrove creeks, sandy flats, and even patch reefs (Sheaves 2005). In particular, these areas are predicted to be severely affected by climate change because of their shallow nature, current high temperatures, and geographic positions, which are strongly affected by tropical storms and hurricanes (Benjamin 2010).

Increasing evidence suggests that fishes located in tropical and sub-tropical regions might be sensitive to minor increases in temperature, due to their evolution in thermally stable environments (Donelson et al. 2011; Sunday et al. 2011). Some species in these regions exhibit a narrow thermal range, which is expected to reduce their ability to cope with temperatures above their thermal optimum (Portner and Farrell 2008). Since fishes have evolved physiologically to live within a specific range of environmental conditions, climate change will force fish to either adapt to increased temperatures or shift their ranges to preferred temperature environments (Roessig et al. 2004). The ability of fish to respond to thermal change is dependent on a number of factors, including thermal history and acclimatization temperature. Each species will exhibit different capacities for acclimatization based on how close they are currently living to their thermal tolerance limits (Portner and Farrell 2008). Fish may be excluded from certain habitats and experience changes in energy allocation at temperatures that approach their critical thermal maxima (Portner and Farrell 2008). While there exists a generic understanding of the potential impacts of climate change on fish physiology, understanding

how temperature will affect fish with different life histories and residing in different regions, like the tropics, is still needed.

Water temperature is a critical determinant of the distribution and abundance of biota through a profound effect on their physiology (Farrell et al. 2008). Important proxies of physiological functions such as swimming performance and scope for activity are valuable tools for exploring fish performance and how it may be mediated by environmental change (Tierney and Farrell 2004; Johansen and Jones 2011). Scope for activity is the difference between routine and maximum metabolic rates, where the maximum metabolic rate is the fish's oxygen consumption at critical swimming speed (Lee et al. 2003). The operational definition of routine metabolic rate for this study was a metabolic rate that incorporates neither locomotion nor digestion, and is measured while the fish is resting early morning, prior to experimentation (MacNutt et al. 2006). Scope for activity and swimming speed, like many physiological functions, have species-specific optimal temperatures that are near a species' preferred or acclimated temperature (Portner and Knust 2007). Both scope for activity and critical swimming speed decrease at temperatures above and below the optimal temperature for that particular species. Reductions in scope for activity and swimming performance have consequences for processes such as foraging, reproduction, growth and escape from predators (Donelson et al. 2011; Clark et al. 2013) and may also lead to metabolic collapse (Farrell et al. 2008). Therefore, whole-animal tolerance and survival to temperature extremes is restricted as energy allocation is limited (Farrell et al. 2008) such that extreme temperatures can affect fitness (Pörtner 2002). Fitness in a changing environment depends on both tolerance (survival probability as a function of temperature) and performance (the capacity to reproduce at various temperatures) (Huey and Kingslover 1989).

An example of a sub-tropical/tropical species that is both an ecologically and economically important sport fish (see Danylchuk et al. 2007a; Fedler 2010, respectively) is the bonefish (*Albula vulpes*). Bonefish inhabit coastal marine environments from nearshore shallows to offshore waters (Humston et al. 2005; Murchie et al. 2013). Bonefish move in and out of mangrove creeks with the incoming and outgoing tides, using these creeks for their abundance of prey and protection from predators (Danylchuk et al. 2007a; Murchie et al. 2013). Recreational bonefishing can

easily support the economy of coastal communities in small island nations, such as The Bahamas, where tourism is responsible for 60 % of the gross domestic product (Fedler 2010). Is it estimated that catch-and-release bonefishing generates approximately $141 million USD annually for The Bahamas (Fedler 2010). Because bonefish often reside in large schools, feed primarily on benthic invertebrates and move with the tides, this species of fish also plays an integral role in the ecology of shallow marine flats (Colton and Alevizon 1983; Ault et al. 2008). Despite their recognized importance, there is limited information on their swimming performance, field generated thermal preferences, as well as energetics, especially when compared to other species targeted by recreational anglers (but see Murchie et al. 2011b, 2013).

Previous work suggests that at high temperatures that approach the critical thermal maxima of bonefish, they tend to avoid creek habitats. Using acoustic telemetry and respirometry, Murchie et al. (2011a) studied the thermal biology of bonefish and found their critical thermal maximum (CT_{max}) was 36.4±0.5 and 37.9± 0.5 °C for fish acclimated to 27.3±1.3 and 30.2± 1.4 °C, respectively. Those tolerances were below maximal temperatures recorded in the tidal creek habitats where bonefish frequently reside (i.e., up to 40.6 °C) (Murchie et al. 2011a). The study by Murchie et al. (2011a) was limited in that bonefish could only be associated with water temperatures when they were within the footprint of the acoustic telemetry array. Given that many tagged bonefish left the footprint of the array for months at a time, it is unclear the temperatures that bonefish face on an annual basis. Indeed, such information on the annual thermal biology of bonefish could provide additional insight into their distribution as well as their bioenergetics, which ultimately drives growth and reproductive investment. Technology has recently improved such that small thermal loggers that can be implanted in fish providing the opportunity to reconstruct complete thermal histories.

The goal of this research was to generate knowledge on the environmental physiology of bonefish with a specific focus on swimming energetics and thermal ecology. To accomplish this goal, we conducted two complementary series of experiments in both the laboratory and field. The laboratory study used a swim tunnel respirometer to define bonefish swimming energetics with respect to temperature, and to identify thermal optima and critical temperatures. The field study used thermal biologgers implanted into wild, free-swimming bonefish to define their annual thermal experience. Together results from these two experiments can be combined to define habitat use and distribution in relation to physiological capacity and potential climate change scenarios.

Materials and methods

Study area and fish collection

This study was conducted along the north shore of Cape Eleuthera, Eleuthera, The Bahamas (24°50′05″ N; 76°20′32″ W) as well as at the Cape Eleuthera Institute (CEI) research facility. The shoreline in this area is composed of tidal creeks, sandy bays, mangrove outcroppings, and sharp calcium carbonate outcroppings (Danylchuk et al. 2007b). Bonefish, *Albula vulpes*, were captured from local tidal mangrove creeks (see Danylchuk et al. 2007b for a description of sampling sites) on an outgoing tide using a large seine net (13 mm mesh, 46 m long; 32 mm mesh, 76 m long; 70 mm mesh, 61 m long) (Murchie et al. 2009). Following capture, bonefish were transferred into a flow-through holding pen (1.3×0.8×1.25 m tall, 31 mm extruded plastic mesh) to provide them with ample oxygen and facilitate handling. All research was conducted in accordance with the policies of the Canadian Council on Animal Care as administered by the Carleton University Animal Care Committee (Protocol B10-06).

Swim tunnel—fish transportation and holding

Bonefish (average 405 mm fork length; range=336–507 mm, weight range=450–1603 g) were transferred to coolers on a boat for transportation back to the CEI seawater facility. Water changes were performed periodically (approximately every 5 min) en route back to the facility using protocols described by Murchie et al. (2009). Fish were held at CEI in a large, aerated holding tank (13 180 l), with mean water conditions of pH 8.3± 0.2, 6.2±0.5 mg/l dissolved oxygen, 36.7±1.0 ppt salinity, and 0.25±0.25 ppm ammonia, at ambient water temperatures. Fish were given a minimum of 24 h to acclimate to laboratory conditions before experimentation.

Swim tunnel

Fish were swum in a 108.74 l modified Blazka-type swim tunnel, similar to that described by Booth et al. (1997). The transparent swim chamber had a 31.9 cm internal diameter and was 136 cm in length, with a plastic grid at each end. The laminar water current in the tunnel was produced by a Leeson Washguard 3-phase AC motor (Leeson Electric Corp., Grafton, Wisconsin, USA, model C182T17WK3D) attached to a Leeson Speedmaster adjustable speed motor controller (model 174526, 0–120 Hz) whose readings (Hz) were calibrated with known water velocities, as measured with a mechanical water flowmeter (General Oceanics, Miami, FL).

Swimming protocol

Individually, fish were moved to the swim tunnel where they recovered overnight (~12 h) at a water speed of 1 cm/s (Lee et al. 2003). The following day, each bonefish performed a modified ramp-U_{crit} test to quantify critical swimming speed (Jain et al. 1997). The ramp-U_{crit} protocol involves increasing water speed in 15 cm/s increments every 15 min until exhaustion. Although 15 min is shorter than the periods often used for salmonids (expect in the case of repeat ramp protocols; e.g., Jain and Farrell 2003), as a greater diversity of species are studied there has been need to modify interval duration to account for diversity of species capabilities (e.g., Nelson et al. 2003; Fisher et al. 2005; Walsh et al. 2006). Exhaustion was deemed to have occurred when the fish's tail touched the back grate for more than 20 s of sustained contact.

U_{crit} values were calculated as described by Brett (1964):

$$U_{crit} = ui + \left(\frac{ti}{tii} \times uii \right),$$

where ui is the water velocity of the last fully completed increment (cm/s); uii is the water velocity increment (15 cm/s); ti is the time the fish swam at the final water velocity (min); and tii is the prescribed period of each water velocity increment (15 min). After each trial, swimming speeds were corrected for the solid blocking effect according to the calculations by Bell and Terhune (1970):

$$Corrected\ U_{crit} = U_{crit}$$
$$\times \left\{ 1 + [0.4FL/0.5(w+d)] \times (0.25\pi dw/At)^{1.5} \right\}$$

where FL is fork length (cm), w is maximum fish width (cm), d is maximum fish depth (cm) and At is tunnel cross-sectional area.

Swim tunnel oxygen consumption measurements

An OxyGuard oxygen probe (OxyGuard Handy Polaris 2, portable DO meter, Water Management Technologies, Inc. Baton Rouge, LA, USA) housed outside the swim tunnel was used to measure oxygen concentrations to 0.1 mg/l resolution. Two aerobic metabolic rate measurements were taken during each experiment; 1) routine $\dot{M}O_2$ and 2) maximum $\dot{M}O_2$. Measuring oxygen consumption immediately prior to experimentation provided routine $\dot{M}O_2$ measurements. Routine $\dot{M}O_2$ did not incorporate locomotion or digestion, water speeds were at 1 cm/s to recirculate the water, but the fish were not swimming during this measurement. Oxygen consumption measured at U_{crit} was designated as the maximum $\dot{M}O_2$ measurement (Lee et al. 2003). The relationship between swimming speed and O_2 consumption was also measured at all speed increments. The first 10 min of each water speed increment was used for measuring oxygen consumption, which was long enough to record a distinctive decrease, without surpassing more than a 30 % decline in dissolved oxygen concentrations. The last 5 min of each water speed increment was used to flush the swim tunnel and replenish oxygen concentrations. The swim tunnel was thoroughly rinsed between experiments with freshwater and background oxygen measurements taken weekly without a fish in the tunnel revealed no detectable change in $[O_2]$.

The rate of oxygen consumption (mgO_2/min/kg) was calculated as:

$$\dot{M}O_2 = \Delta[O_2]v/mt,$$

where oxygen concentration $[O_2]$ is measured in mgO_2 /l, v is swim tunnel water volume (total swim tunnel volume minus the fish's volume, assuming 1 kg=1 l), m is the fish's weight (kg), and t is time (min). Scope for activity was then calculated as the difference between $\dot{M}O_{2max}$ and $\dot{M}O_{2routine}$ (Lee et al. 2003; Clark et al. 2013).

To minimize handling stress influence on swimming performance and respiration, fish were weighed (kg) and, measured for fork length (FL; cm), total length (TL; cm), width (w; cm) and maximum depth (d; cm) after the trials and then released.

Swim tunnel temperature manipulation

Experiments occurred between October 16, 2012, and November 5, 2013, at ambient water temperatures (20.7–30.3 °C), thereby permitting us to define variation in swimming performance and metabolic scope across different water temperatures and seasons. Water temperature was kept as constant as possible during the protocol for any one fish (range=0.4–1.5 °C). Additional experiments were performed during the summer at adjusted higher temperatures. Heaters were used to gradually increase water temperatures during overnight swim tunnel acclimations to a maximum of ~6 °C above ambient to extend the temperature range (Lee et al. 2003). Adjusted treatment temperatures ranged between 30 and 36 °C to stay below bonefish CT_{max} of 37.9 °C (Murchie et al. 2011a).

Laboratory study data analysis

Regression analyses and a polynomial quadratic equation was fitted to the critical swimming speed and scope for activity figures in relation to temperature, as well as the net cost of transport figure, in relation to swimming speed (Eliason et al. 2013). Net cost of transport was calculated from scope for activity divided by water velocity for each swimming speed and was used to provide an index of overall swimming efficiency (Lee et al. 2003). Optimal temperature (T_{opt}) was defined as the temperature corresponding to the vertex of the polynomial regression between critical swimming speed and temperature, and between scope for activity and temperature (Eliason et al. 2013). The upper critical temperature (T_{crit}) was defined as the temperature where both critical swimming speed and scope for activity reached zero. $P<0.05$ was used to establish statistical significance. The effect of speed and temperature on bonefish metabolism was analyzed using a linear mixed effects model with swimming speed (cm/s), temperature (°C), fork length (cm), and the interaction between swimming speed and temperature as predictors and individual fish as a random factor. Backward model selection was used with log-ratio tests to determine significant terms, and models were validated following the protocol of Zuur et al. (2009). All statistics were performed using SigmaPlot 11.0 (www.systat.com) and R (www.r-project.org).

Thermal logger implantation

Bonefish (389±3 mm fork length; mean±SD; range= 308–480 mm) were captured between May 11 and June 23, 2012, from local mangrove creeks using the same seine net methods as described above (Murchie et al. 2009). A total of 138 bonefish were surgically implanted with thermal loggers at the capture site (iButton DS1921H, factory stated resolution=±0.1 °C, accuracy=±1 °C, range=−55 °C to +100 °C, Maxim Integrated Products, Inc., San Jose California, USA) to record temperature every 255 min for 362 days. Thermal loggers were waterproofed using Plasti Dip (Performix Brand, Blaine MN) and had a diameter of 16 mm, a height of 5 mm and a weight of ~1 g. Plasticized temperature loggers were tested in a laboratory setting to have an accuracy of 0.4±0.3 °C and a temperature precision of 0.2±0.3 °C (Donaldson et al. 2009). Prior to surgery, individual bonefish were removed from the holding pen, and placed in a 100 l cooler with sufficient MS-222 concentrations to anesthetise bonefish in less than 2 min. After sustained equilibrium loss, bonefish were placed supine on a piece of foam covered with anti-slip material on top of a recirculating surgery table. The fish's gills were constantly supplied with fresh seawater using a recirculating pump. Surgeons wore vinyl gloves, and thermal loggers, along with surgical tools, were cleaned with iodine prior to every surgery. To implant the thermal loggers, a 1–2 cm midline ventral incision was made posterior to the pectoral girdle (Wagner et al. 2011). Each incision was closed with two simple interrupted sutures (Ethicon 3-0 PDS II, monofilament absorbable suture material, Johnson and Johnson, New Jersey). Fish were then measured for fork length (to the nearest mm) and tagged in the dorsal musculature of the fin rays for visual identification of iButton fish (Hallprint plastic tipped dart tags, PDS) (Ault et al. 2005). Surgical procedures lasted less than 5 min per fish and were always conducted by the same surgeon (as per Cooke et al. 2011a). Post-surgery, fish were transferred to a recovery flow-through holding pen (1.3×0.8×1.25 m tall, 31 mm extruded plastic mesh) for a minimum of 1 h. Following the recovery period, all bonefish were released at the capture site together to encourage schooling and protection from predators.

After being at liberty with an implanted iButton, eight bonefish were recaptured from local creeks between July 16, 2012 and April 9, 2013 with multiple

seining events, all of which followed procedures described above. Fish were lethally sampled to retrieve thermal loggers, sex and measure the fish. iButtons were downloaded for analysis. Thermal loggers were also strategically placed within the mangrove creeks inhabited by bonefish to define environmental water temperatures.

Thermal logger data analysis

Data from iButton thermal loggers recovered from the bonefish were imported into a database. Factors predicting temperature patterns were defined using a generalised additive model (GAM). GAMs and their mixed-model counterpart GAMMs, are semi-parametric extensions of generalized-linear models with the ability to deal with highly non-linear and non-monotonic relationships between a response and a set of explanatory variables (Hastie and Tibshirani 1990; Guisan et al. 2002; Wood 2006). Preliminary analyses using generalized linear models showed non-linear patterns in the residuals when plotted against day and hour, thus indicating that a GAM was an appropriate analysis for these data (Wood 2006; Zuur et al. 2009). The influence of ten different terms on fish temperature data were tested, including: hour of the day, centered fork length, sex, tide, season, fish ID, centered fork length × sex, tide × hour, tide × day, and season × hour. A dependency structure was added to the model to account for serial correlation between observations within the same animal (Pinheiro and Bates 2000; Zuur et al. 2009). The correlation structure was incorporated using the mixed-modelling extension of GAM in the mgcv package for R (Wood 2006). Individual accumulated thermal units were also generated to assess differences between sexes of fish. An accumulated thermal unit is the daily cumulative temperature above 0 °C experienced by each fish (Crossin et al. 2008). A logistic regression of tag retention was used to define the duration of time when bonefish began to expel thermal loggers.

Results

Laboratory—swim tunnel

Regression analyses showed a significant ($P<0.05$) bell-shaped relationship between U_{crit} and temperature

(Fig. 1a, b) and similar, although weaker, bell-shaped relationship between scope for activity and temperature (Fig. 1d). Optimal swimming temperatures were defined as the temperature corresponding to the vertex of the regressions between U_{crit}, scope for activity and temperature. Critical swimming speed was optimal at 28 °C ($N=69$) while scope for activity was optimal at 26.7 °C ($N=49$) (Fig. 1). The upper critical temperature for both U_{crit} and scope for activity was 36 °C (Fig. 1). At this temperature fish would not swim and later died. Critical swimming speed at T_{opt} was 96 cm/s or 2.4 BL/s while scope for activity at T_{opt} was 7.5 mgO$_2$/min/kg (Fig. 1).

Bonefish oxygen consumption (MO$_2$) increased linearly with increasing swimming speed and water temperature, and decreased with increasing fish size (i.e. small fish in high temperatures had the highest MO$_2$; Fig. 2). Swimming speed (cm/s), temperature (°C) and fork length (cm) were all significant predictors of metabolic rate, where $MO_2 = 2.42 + 0.09 \times speed + 0.25 \times temp - 0.14 \times FL$ (Table 1). The relationship between swimming speed and net cost of transport (COT$_{net}$) showed a U-shaped curve. The lowest cost of transport was defined as the swimming speed corresponding to the pit of the regression. The lowest cost of transport (0.08 mgO$_2$/min/kg) for bonefish was a swimming speed of 70 cm/s (Fig. 3).

Field—thermal loggers

Of the 138 bonefish implanted with thermal loggers, eight were recaptured with useable data, with an equal number of each sex (Table 2). None of the wild, free-swimming bonefish exceeded temperatures of 36 °C, which corresponds to their upper critical temperature determined with the swim tunnel (Fig. 4). On a seasonal basis, bonefish experienced an average temperature of 27±2.3 °C (min=22.7 °C, max=33.5 °C) in the spring, 30±2.6 °C (min=24.4 °C, max=35.7 °C) in the summer, 25±2.7 °C (min=18.8 °C, max=32.8 °C) in fall, and 23±2.4 °C (min=16.1 °C, max=29.7 °C) in winter (Fig. 4). Bonefish experienced fluctuations of up to 14 °C per season and up to 8 °C per day. A clear and drastic decline in temperatures can also be seen between September and November, corresponding with Hurricane Sandy, which passed through The Bahamas on October 22, 2012 and dissipated on October 31, 2012 (Fig. 4).

The best model to explain bonefish thermal experience contained hour of the day, fish ID, and hour of the
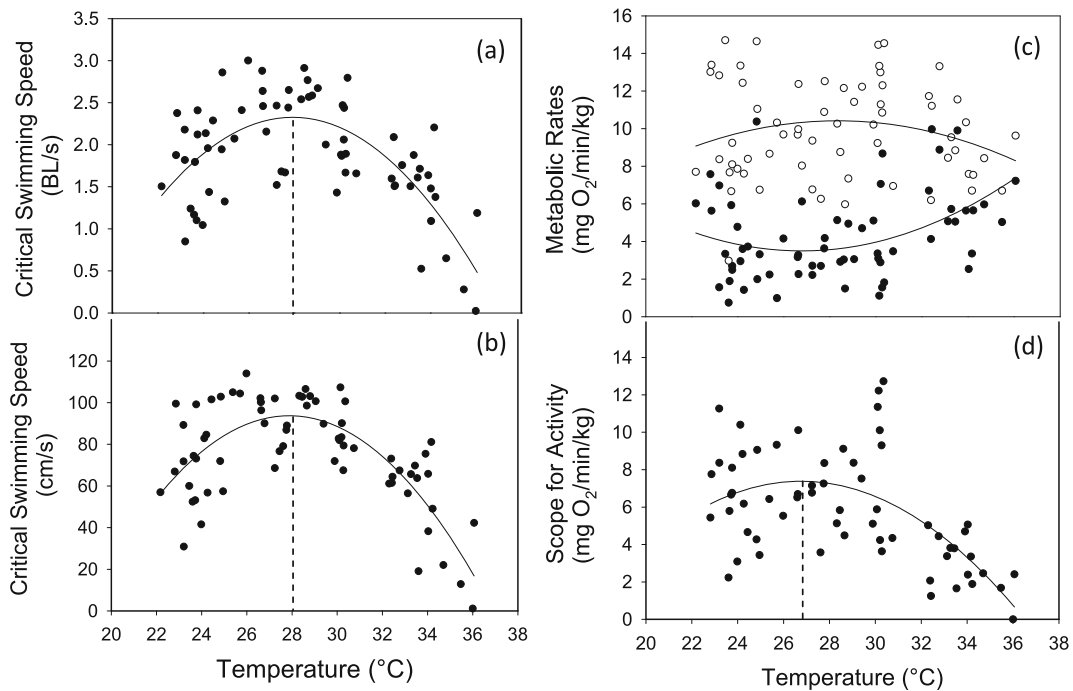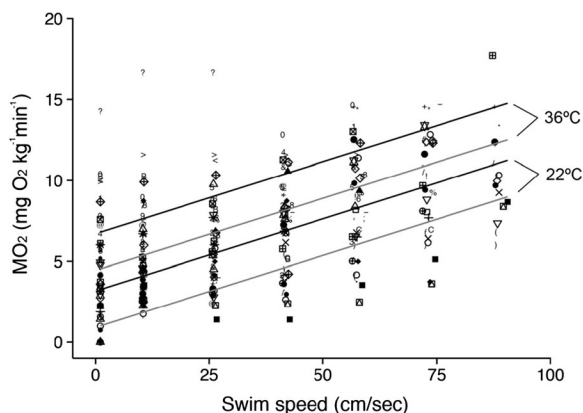
Fig 1 **a** Critical swimming speed in BL/s in relation to water temperature for bonefish. **b** Critical swimming speed in cm/s in relation to water temperature. **c** Routine (*black circle*) and maximum (*white circle*) oxygen consumption (MO_2) in relation to water temperature. **d** Scope for activity, the difference between maximum and routine metabolic rates, for individual fish from **c** in relation to water temperature. Every *data point* represents an individual bonefish and *vertical dotted lines* represent optimal temperatures. Polynomial quadratic equations were fitted to **a**

critical swimming speed (BL/s) ($y=-19.5+1.6x+-0.03x^2$; $r^2=0.47$,$P<0.001$) (95 % CI: 0.08, 0.01), **b** critical swimming speed (cm/s) ($y=-799.4+64x+-1.2x^2$; $r^2=0.56$,$P<0.0001$) (95 % CI: 3.69, 0.90), **c** routine metabolic rate ($y=35.7+-2.4x+0.04x^2$; $r^2=0.16$,$P=0.006$) (95 % CI: 0.03, 0.32), maximum metabolic rate ($y=-18.1+2.0x+-0.04x^2$; $r^2=0.04$,$P=0.33$) (95 % CI: 0.20, 0.14) and **d** scope for activity ($y=-48.3+4.2x+-0.08x^2$; $r^2=0.35$, $P<0.0001$) (95 % CI: 0.52, 0.18)

day × season as significant predictors (Table 3). The model with a dependency structure was a significant

Fig 2 Rate of bonefish oxygen consumption (MO_2) across a range of swimming speeds, as well as temperature and fork length as significant predictors of metabolism. *Grey lines* represent the upper size range (50 cm) and *black lines* the lower size range (34 cm) of bonefish fork length

improvement over the model without (df=1, *L*-ratio= 5663.5, $P<0.0001$). The contribution of the smooth term (day of year) was highly significant and illustrated clear patterns associated with the astronomical seasons ($P<0.0001$, Fig. 5). As seen in Fig. 5, temperatures across the summer were fairly consistent whereas temperatures dropped significantly with the progression of fall and stayed low throughout the winter.

Despite the utility of thermal logger implantation as a means for collecting thermal profiles of wild bonefish,
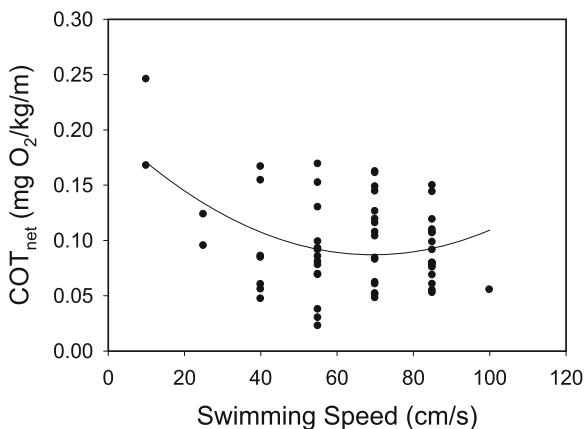
Table 1 Significant predictors of metabolism

	Value	Std. error	DF	*t*-value	*p*-value
(Intercept)	2.422	3.458	300	0.700	0.484
Speed	0.089	0.006	300	14.721	0.000
Fork length	−0.140	0.062	64	−2.255	0.027
Temperature	0.252	0.069	64	3.651	0.0005

Fixed effects: O_2 ~ speed + FL + temperature

Fig 3 Relationship between net cost of transport (COT_{net}) and swimming speed for bonefish. A polynomial quadratic equation was fitted to COT_{net} ($y=0.2+-0.003x+2.37E-005x^2$; $r^2=0.16$, $P=0.0079$), although it was insignificant ($p=0.03$, $R^2=0.07$)

there are a few previously unforeseen disadvantages. Of the 17 fish recaptured, five fish had expelled their thermal loggers and four loggers recovered had errors and no data, leaving only 8 recaptured fish with useable data. After 220 days at liberty, more than 55 % of the bonefish recaptured had expelled their thermal loggers (Fig. 6).

Discussion

This study represents the first to quantify the role of temperature on swimming energetics of bonefish in both the field and laboratory. Most other studies to date that used swim tunnels to determine critical swimming speed and scope for activity have focused on salmon and the

effects of temperature on migration and spawning success (i.e., Lee et al. 2003; Eliason et al. 2011). By combining the laboratory and field studies, these data enabled us to determine if the temperatures bonefish experience correspond to their thermal optima. Laboratory-derived measurements of thermal optima were compared to temperatures from within the tidal creek habitats to examine habitat use and the potential effects of climate change. Given the ecological and economic importance of bonefish, a lack of information on their thermal tolerances demanded an investigation into their thermal biology. Collectively these data also provide the opportunity to generate a complete bioenergetics model of bonefish when coupled with activity levels (i.e., from Murchie et al. 2011b).

Swimming performance and respiratory energetics

Swimming performance and scope for activity are often used as a proxy for quantifying fish fitness in an ecologically relevant way (Plaut 2001; Donelson et al. 2011). In most fish species, critical swimming speed (U_{crit}) and scope for activity are reduced at lower temperatures, increase to an optimum peak and decrease again as temperatures approach the species upper thermal limit (Claireaux et al. 2006). As expected, as temperatures exceeded bonefish thermal optimum, both critical swimming speed and scope for activity for bonefish declined. For bonefish, 28 °C was the optimum temperature for U_{crit} and 26.7 °C was the optimum temperature for scope for activity. The difference between the optimal temperatures for critical swimming speed and scope for activity is small but still challenges

Table 2 Summary of tagging and biological data for the eight recaptured iButton fish used in this study

iButton	Sex	Fork length (mm)	Date tagged	Date recaptured	# days at large	ATU
111	F	352	23-Jun-12	11-Mar-13	335	149
56	M	430	12-May-12	07-Mar-13	267	148
33	M	424	11-May-12	11-Jan-13	258	154
34	F	410	11-May-12	11-Jan-13	174	149
105	F	450	23-Jun-12	16-Jan-13	170	160
114	F	465	23-Jun-12	11-Jan-13	137	164
124	M	439	23-Jun-12	06-Sep-12	87	175
90	M	408	29-May-12	06-Sep-12	47	166

Individuals are listed in decreasing order of how long they were at liberty. Accumulated thermal units (ATU) are presented as means of the cumulative daily water temperatures. All captured fish originated in Broad creek and fish were recaptured in that same creek or the adjacent Kemps creek
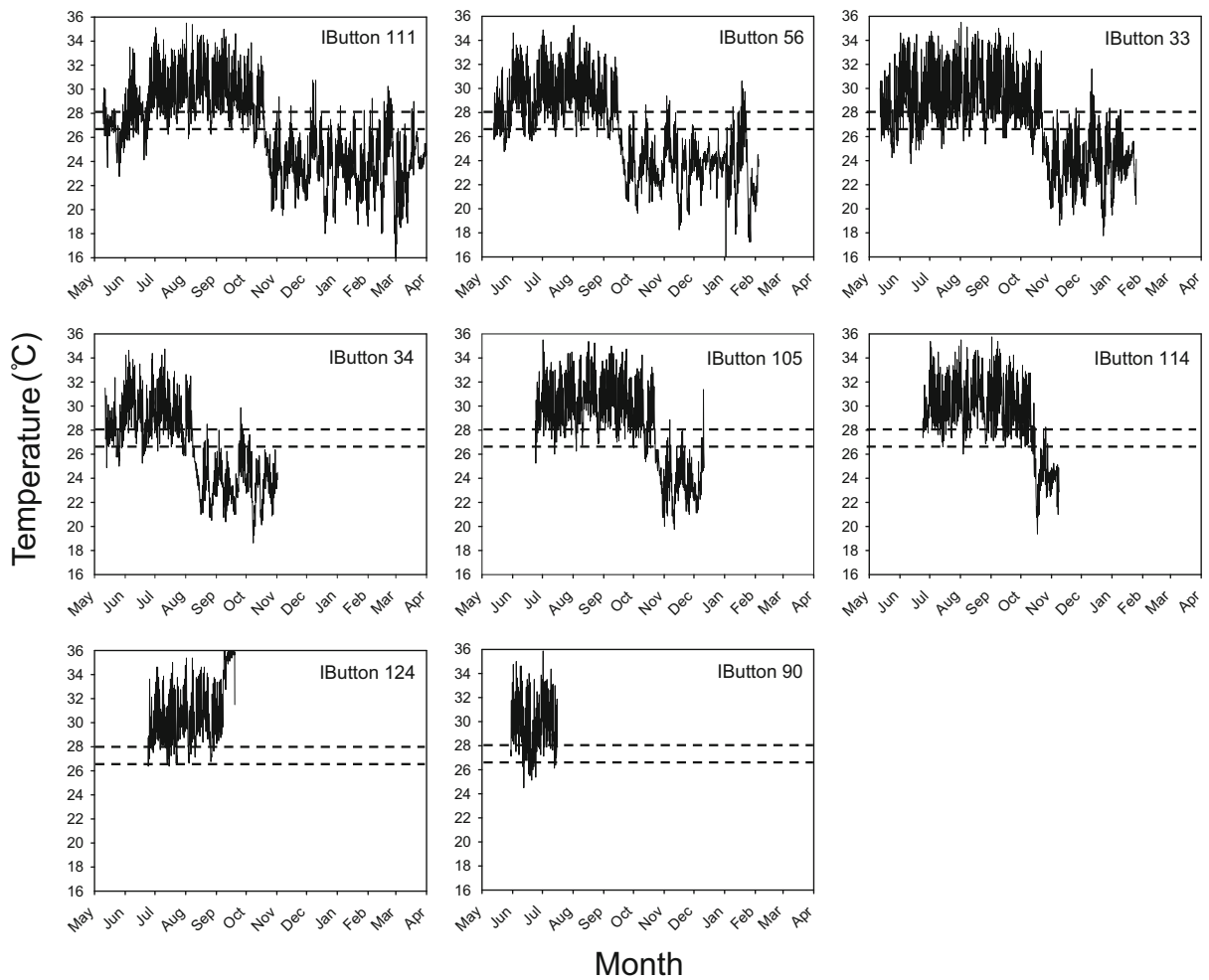
Fig 4 Thermal profiles of the eight recaptured bonefish with iButton thermal loggers. The dates represented are between May 11, 2012 and March 11, 2013. *Dotted lines* represent optimal temperatures for critical swimming speed (28 °C) and scope for activity (26.7 °C)

the oxygen and capacity limited thermal tolerance (OCLTT) hypothesis that scope for activity is an over-arching physiological process that governs most other performances (i.e., including swimming performance, growth, digestion, reproduction, immune function, muscular activity, behaviour) (Portner 2001; Clark et al. 2013). The OCLTT concept suggests that all

physiological performances will be optimized at the scope for activity optimal temperature, and ultimately optimise fitness (Eliason et al. 2011; Clark et al. 2013). However, an alternative theory, proposed by Clark et al. (2013), is the idea of 'multiple performances—multiple optima' (MPMO), where different physiological functions have different optimal temperatures, which could be the case in this study (Portner and Farrell 2008).

For both U_{crit} and scope for activity, the maximum critical temperature for bonefish was 36 °C. This temperature was slightly lower than previously reported bonefish critical temperatures of 37.9±0.5 °C for fish acclimated to 30.2±1.4 °C (Murchie et al. 2011a). However, both these studies used loss of equilibrium as their proxy for determining critical temperatures, instead of a physiological performance, such as

Table 3 The importance of individual fixed terms for the model to predict the thermal experience of bonefish

Model term	L-ratio	DF	p-value
Hour	231.1	5	<0.0001
Fish ID	1301.3	7	<0.0001
Season: hour	98.3	3	<0.0001
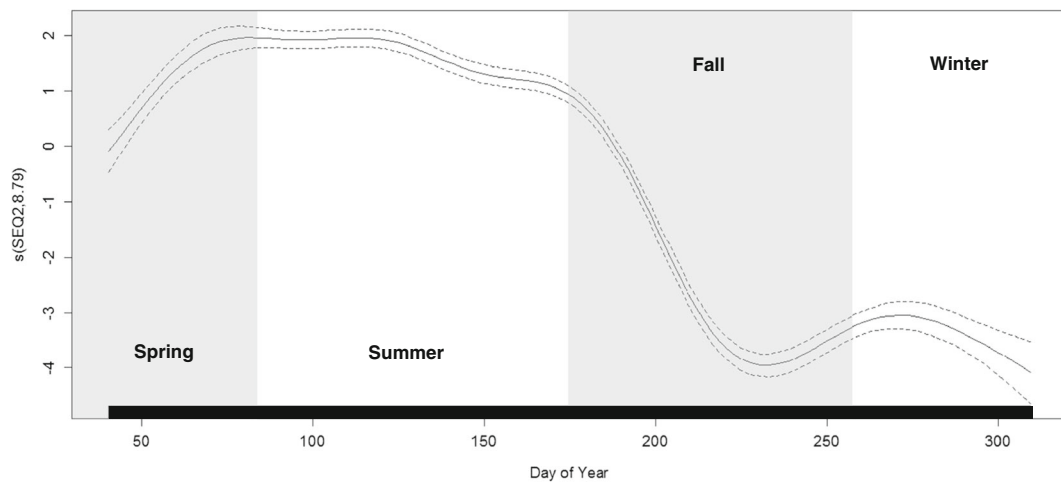
Fig 5 Estimated smoothing curves generated for bonefish thermal experience. *Solid dark lines* are the fitted values while dashed lines represent the approximate 95 % point-wise confidence limits. A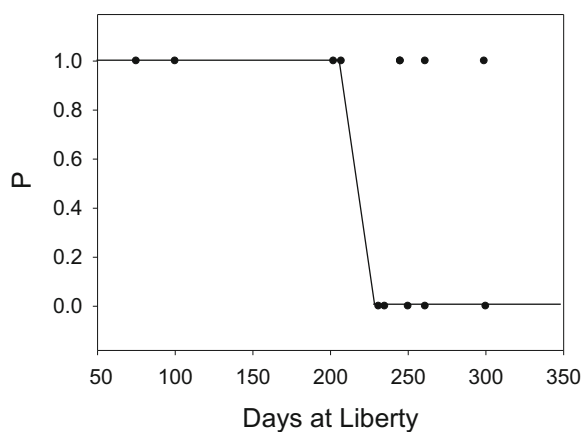pproximate significance of the smoothing term was $F_{8.79}$ = 110.4, $P<0.0001$. Model degrees of freedom are taken as the trace of the influence matrix for the model fit. Time is divided into daily intervals, separated by 50 days, with the first day starting at 38, which is May 9, 2012

swimming speed. In comparison to other species, bonefish thermal tolerances and critical temperatures are relatively low. For instance, 22 species of freshwater fish found in North America exhibited a CT_{max} of 40 °C or higher, including largemouth bass (Beitinger et al. 2000). Although limited data exists for tropical marine species, there are still some species with which comparisons can be made. For 15 species of reef fish, including wrasses, snappers, cardinalfish, gobies, mojarra and many others, maximum critical temperatures ranged between 34.7 and 40.8 °C (Mora and Ospina 2001). Therefore, bonefish thermal tolerances are typical, if not low, compared to other near-shore dwelling sub-tropical species.

Fig 6 Logistic regression of iButton retention (represented by 1) and iButton expulsion (represented by 0) in bonefish at liberty

At the bonefish's optimal temperature, U_{crit} was 96 cm/s or 2.4 BL/s and their highest recorded U_{crit} in this study was 114 cm/s or 3.0 BL/s. In comparison to multiple stocks of sockeye and coho salmon whose U_{crit} ranged between 89.9–136.6 cm/s or 1.4–2.3 BL/s, bonefish critical swimming speeds are relatively impressive (Lee et al. 2003; Brownscombe et al. 2014). While salmon must make upstream migrations for spawning, bonefish live in high predator areas with limited cover, resulting in high swimming speeds for predator escape.

Thermal biology of bonefish in the field

According to the iButton thermal profiles, on an annual basis, bonefish did not experience temperatures below their lower critical threshold, 14.5 °C or above their upper threshold, 35.8 °C ($N=8$). The temperatures recorded in this study ranged between 15 and 38 °C in the creeks, and have even been recorded up to 40.6 °C by Murchie et al. (2011a). The shallow nature of tidal mangrove creeks makes them vulnerable to higher temperatures and when creek temperatures exceed bonefish CT_{max} they are thermally excluded from their feeding habitats. According to their thermal profiles, the mean temperature bonefish experienced was 28.1 °C, which also corresponds to their optimal temperature for U_{crit}. There is significant inter-individual variation in temperature experience for bonefish, which has been observed for Pacific salmon (Drenner et al. 2014). According to Danylchuk et al. (2011) bonefish moved from their

shallow flats to aggregations near a deep water drop-off, indicative of spawning; this occurred during full and new moons, primarily between October and May. This spawning period corresponds with the considerably lower temperatures experienced by bonefish throughout the winter months. While bonefish spawning is clearly linked to the lunar cycle (Danylchuk et al. 2011), it could also reflect a need for lower temperatures when their scope for activity is reduced. The bonefish thermal profiles also showcase a drastic and seemingly sudden decline in temperatures between September and November. This temperature decline corresponds to Hurricane Sandy, which passed through The Bahamas between October 22 and October 31, 2012.

Model selection showed that hour of the day, fish ID, and hour of the day × season were the only significant terms to explain temperature experience. There were no sex related differences that could be attributed to the small sample size (four male and four female). The fact that day versus night was not a significant predictor of temperature was not surprising as bonefish movement patterns are more often associated with tidal cycles (Humston et al. 2005). Bonefish in The Bahamas regularly move into mangrove creeks at high tide to feed and then escape to deeper water during low tide (Murchie et al. 2013). However, tides were not a significant predictor of bonefish temperature. This may be due to the fact that bonefish utilize creeks at high tide when the temperature difference between the creeks and deeper water would be smallest. During certain months and seasons bonefish in The Bahamas are consistently above their optimal temperature, while during other seasons, bonefish are consistently below their optimal temperature. These data illustrate how flexible fish are relative to the laboratory-derived estimates of thermal optima. While it obviously is not expected that fish will consistently remain at optimal temperatures, it does suggest that many other factors contribute to fish habitat selection and dictate behaviour other than temperature, such as light, foraging, and predator avoidance.

Climate change

Organisms living in tropical and sub-tropical marine environments reside in relatively thermally stable environments and are therefore often physiologically optimized in a narrow thermal range (Johansen and Jones 2011). While these specializations can have a selective advantage over phenotypic flexibility in terms of growth

and reproduction, they can also be disadvantageous if significant thermal changes occur (Johansen and Jones 2011). Now knowing the thermal window for bonefish in The Bahamas, it is worth considering the potential consequences of climate change. According to the Intergovernmental Panel on Climate Change (IPCC) average global sea surface temperatures are projected to increase between 1.8 and 4.0 °C per 100 years depending on the scenario of carbon dioxide concentrations (Stocker et al. 2013). Using the predictions by the IPCC the effects of climate change on bonefish thermal habitat can be determined. The percentage of time tidal creek temperatures currently exceed bonefish T_{opt} and T_{crit} are 54 and 0.51 %. By applying temperature increases of 1, 2, 3 and 4 °C to current data, it can be projected that under climate change scenarios, temperatures will exceed bonefish T_{crit} 1.48, 2.88, 5.40 and 9.58 % of the time, respectively. Discounting the potential for acclimation and adaptation, the laboratory and field data suggest that bonefish occupy habitats that approach their T_{crit} and that even a 1 °C shift in temperature may represent a relatively large shift away from bonefish T_{crit}. When temperatures exceed bonefish T_{crit} they can be thermally excluded from their tidal mangrove creek habitats. During these times, bonefish will be forced out of foraging in the protective shallow creeks and into deeper waters where predator exposure is higher. In addition to potentially being thermally excluded from creek habitats at certain high temperatures, compounding stressors such as increased recreational fishing and changes in habitat quality could make bonefish and tropical tidal creek fish particularly vulnerable to climate change (Murchie et al. 2011a). While there is the potential for individual bonefish to acclimate to water temperature changes, on a population scale the species may be less tolerant (Murchie et al. 2011a). Additional research is needed to quantify temperature resilience and adaptability to temperature change as well as energetic tradeoffs associated with occupying thermally dynamic habitats. Recent findings support that models based on the optimal temperature for U_{crit} and scope for activity will improve predictions of population fitness under global climate scenarios (Portner and Knust 2007).

Tag expulsion

It is interesting that more than 55 % of the bonefish recaptured had expelled their iButton thermal loggers

after 220 days at liberty. This can be remedied in the future by concentrating recapture efforts earlier than the 220 day bench mark. More importantly, this finding suggests that biotelemetry studies, which are common for bonefish (e.g., Humston et al. 2005; Murchie et al. 2013), may be unlikely to be successful in the long-term. Few studies have been able to track bonefish across multiple years (although admittedly many fail to identify the longevity of the tag to know the extent to which that is possible) and they often conclude that "missing tags" indicate that fish have left the vicinity where animals can be tracked or that fish have experienced mortality. The data from our study suggest that expulsion of tags may occur which requires caution when using intracoelomic implantation for long-term tagging studies on bonefish. Interestingly, tag expulsion is a well-known phenomenon in freshwater fish (reviewed in Cooke et al. 2011b), but fewer examples exist in marine systems. There is a need to conduct long-term tagging validation studies across a wider range of marine fish species to determine the extent to which this may be an issue for marine tracking studies and how it is influenced by different tag coating material.

Conclusion

In summary, bonefish optimal temperatures for critical swimming speed and scope for activity were similar, 28 and 26.7 °C respectively, and their critical temperatures were the same. These laboratory collected data correlated well with field data showing that bonefish did not experience temperatures beyond their critical thresholds and spent the majority of their time in temperatures close to their optima. Our research focused on a single population in The Bahamas. Stock-specific differences in thermal optima and tolerances of Pacific salmon are well documented (e.g., Lee et al. 2003; Farrell et al. 2008; Eliason et al. 2011) but it is unclear whether the same occurs for bonefish. In addition to need for intra-specific studies, inter-specific comparisons of critical swimming speed and scope for activity would provide a useful method for predicting which species are most susceptible to population declines and range shifts as ocean temperatures increase (Nilsson et al. 2009). Our work suggests that climate change has the potential to induce entire population shifts in fitness in response to temperature change. The information generated here on the optimal and critical temperatures of a species can provide fisheries managers with the potential to develop species specific management strategies in response to predicted climate change through coastal development mitigation and angling restrictions during peak summer temperatures (Portner and Knust 2007; Farrell et al. 2008). Information on the swimming energetics of bonefish can be combined with activity levels of wild bonefish to create a complete bioenergetics model for bonefish. Creating a bonefish bioenergetics model would provide fisheries managers and research with a useful tool for predicting responses of bonefish to ecological change and understanding bonefish conservation (Hansen et al. 1993).

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