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Thermal biology of bonefish (*Albula vulpes*) in Bahamian coastal waters and tidal creeks: An integrated laboratory and field study

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ABSTRACT

Little is known about the thermal tolerances of fish that occupy tropical intertidal habitats or how their distribution, physiological condition, and survival are influenced by water temperature. We used a combination of laboratory and field approaches to study the thermal biology of bonefish, *Albula vulpes*, a fish species that relies on nearshore intertidal habitats throughout the Caribbean. The critical thermal maximum (CTMax) for bonefish was determined to be 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, and these tolerances are below maximal temperatures recorded in the tropical tidal habitats where bonefish frequently reside (i.e., up to 40.6 °C). In addition, daily temperatures can fluctuate up to 11.4 °C over a 24-h period emphasizing the dramatic range of temperatures that could be experienced by bonefish on a diel basis. Use of an acoustic telemetry array to monitor bonefish movements coupled with hourly temperature data collected within tidal creeks revealed a significant positive relationship between the amount of time bonefish spent in the upper portions of the creeks with the increasing maximal water temperature. This behavior is likely in response to feeding requirements necessary to fuel elevated metabolic demands when water temperatures generally warm, and also to avoid predators. For fish held in the laboratory, reaching CTMax temperatures elicited a secondary stress response that included an increase in blood lactate, glucose, and potassium levels. A field study that involved exposing fish to a standardized handling stressor at temperatures approaching their CTMax generated severe physiological disturbances relative to fish exposed to the same stressor at cooler temperatures. In addition, evaluation of the short-term survival of bonefish after surgical implantation of telemetry tags revealed that there was a positive relationship between water temperature at time of tagging and mortality. Collectively, the data from these laboratory and field studies suggest that bonefish occupy habitats that approach their laboratory-determined CTMax and can apparently do so without significant sub-lethal physiological consequences or mortality, except when exposed to additional stressors.

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1. Introduction

Water temperature exerts more control over fish than any other single abiotic factor (Beitinger and Fitzpatrick, 1979; Magnuson et al., 1979) as it influences nearly all biochemical, physiological, and life history activities of fish (Fry, 1967; Brett, 1971) and is a potential source of disturbance (Beyers and Rice, 2002). All fish species have a temperature range within which individuals do not exhibit any signs of stress and/or aversion behavior (Portz et al., 2006). The ability of fish to respond to thermal change is dependent on a number of factors (see Hutchison, 1976), including thermal history or acclimation temperature (Chung, 2001). Each species will exhibit different capacities for acclimation based on how close they are currently living to their thermal tolerance limits (Somero, 2005). Fish inhabiting water bodies that warm gradually in spring/summer and cool in fall/winter may use thermal changes to

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coordinate seasonal activities, whereas fish that migrate between thermally distinct habitats have to adapt to these thermal changes to exploit the new environment (Guderley et al., 2001).

Thermal tolerance data are limited for fish inhabiting tropical marine areas, particularly when compared to those inhabiting temperate regions (Ospina and Mora, 2004). Given the ecological and economic importance of coastal areas (see Holmlund and Hammer, 1999; Moberg and Folke, 1999), coupled with the influence of thermal phenomena such as El Niño and the impact of global warming in these ecosystems (Mora and Ospina, 2001), the lack of information on thermal tolerances demands a broader investigation into the thermal physiology and ecology of fish from the tropics (Roessig et al., 2004). Bonefish (*Albula* spp.) are a group of fishes that occupy subtropical and tropical nearshore areas around the world (Pfeiler et al., 2000). Bonefish are common benthivorous fish in many tropical areas, moving into shallow water habitats (e.g., tidal creeks and 'flats') to feed on invertebrates and small fish during high tide, and then moving into deeper water at low tide (Humston et al., 2005). During these daily movements, bonefish potentially face large shifts in ambient water temperatures as they may occupy waters less than 0.1 m deep (Colton and Alevizon, 1983). In addition, bonefish are the object of a popular sport fishery (Pfeiler et al., 2000). The combination of exposure to diurnal and seasonal fluctuations in water temperatures in tropical waters and exposure to multiple stressors associated with recreational angling (e.g., capture and handling; see Danylchuk et al., 2007; Suski et al., 2007), make bonefish an interesting model for thermal tolerance investigations.

Fish temperature tolerance can either be estimated from field observations or quantified by laboratory studies (Beitinger et al., 2000). Field observations of fish kills resulting from exposure to extreme high or low temperatures or the examination of minimum and maximum water temperatures within a species' natural distribution both provide estimates of a species' thermal tolerance. These approaches, however, are not precise nor do they rule out other potential abiotic or biotic factors that may contribute to the fish's behavior (Beitinger et al., 2000). Because of the limitations of purely empirical studies, two laboratory methods have been accepted universally as the most accurate approach to quantifying temperature tolerances of fish: the incipient lethal temperature technique (ILT) and the critical thermal method (CTM) (Bennett and Judd, 1992; Currie et al., 2004). The CTM approach is the most common index used as lethal temperatures are estimated without actually killing fish (Beitinger et al., 2000). Critical thermal limits are determined as the mean temperature in which individual fish display signs of stress after being exposed to a constant linear temperature change (Mora and Ospina, 2002; Cook et al., 2006). When temperature is increased linearly, the critical thermal maximum (CTMax) is determined. When temperatures are decreased linearly, the critical thermal minimum (CTMin) is attained. Because the upper tolerance limits of a species increase with acclimation temperature (Beitinger and Bennett, 2000), thermal tolerances are typically determined at a number of acclimation temperatures. An issue of growing concern exists, however, in the applicability of laboratory-determined thermal tolerance ranges to fish in natural settings, because diel temperature fluctuations are common in various fish habitats (Wehrly et al., 2007). Vast amounts of literature determining the thermal tolerance of various fish species have been generated (see Beitinger et al., 2000), not only as a result of interest in understanding this critical aspect of fish ecology, but also by the current need to predict the biological effects of climate change (Cook et al., 2006; Mora and Maya, 2006). Unfortunately, there are few studies that link laboratory research on thermal biology with field studies of behavior, or studies that further extend this work to consider the potential impacts of climate change on wild fish.

The purpose of this study was to (1) determine the critical CTMax of bonefish at two different seasonal acclimation temperatures; (2) examine the stress physiology associated with bonefish reaching CTMax; (3) examine the combined effects of thermal stress and capture/holding stress; and (4) link the spatial ecology of bonefish with the thermal regimes experienced in tidal creeks and coastal areas.

2. Materials and methods

This study took place on the island of Eleuthera, The Bahamas (N 24°50′05″ and W 76°20′32″) in the laboratory facilities at the Cape Eleuthera Institute (CEI), as well as in a number of tidal creek
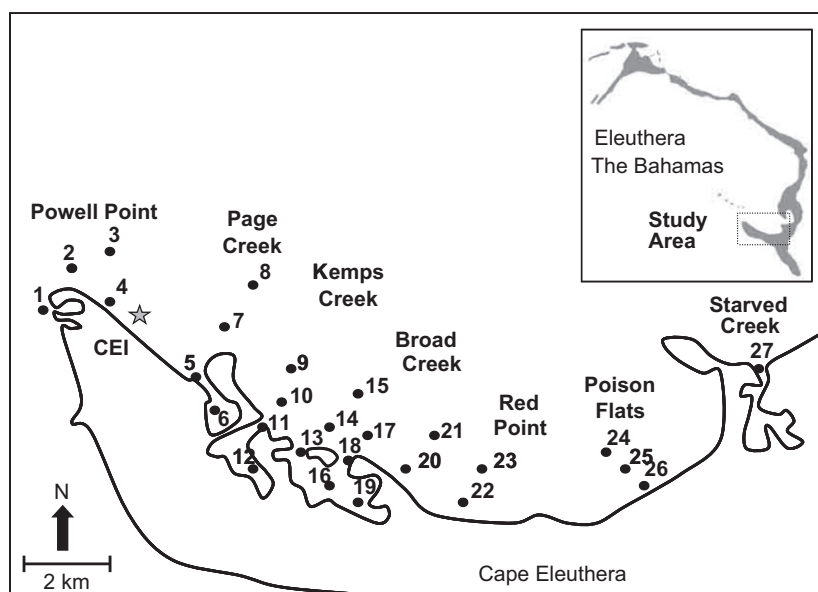

Fig. 1. Study area along the north coast of Cape Eleuthera, Eleuthera, The Bahamas (N 24°50′05″ and W 76°20′32″), showing the locations of the 27 hydrophone receivers (black circles), the various tidal creeks, and the location of the Cape Eleuthera Institute (CEI). Receivers were roughly numbered sequentially from west to east. Hydrophone receivers with associated temperature loggers are #5 and #6 (Page Creek mouth and backwaters, respectively), #11 and #12 (Kemps Creek mouth and backwaters, respectively), and #16, #18, and #19 (the two mouths of Broad Creek and the backwater, respectively). An additional temperature logger, deployed along an open stretch of coastline off of CEI, is denoted by a star. The inset map displays the entire island of Eleuthera with the study area highlighted.

and tidal flats systems adjacent to Cape Eleuthera (Fig. 1). Genetic analyses of bonefish from this area indicated that all bonefish specimens analyzed were *Albula vulpes* (Danylchuk et al., 2007). All experiments were conducted in accordance with the policies of the Canadian Council on Animal Care as administered by the Carleton University Animal Care Committee (Protocol B07-03, 04).

2.1. Laboratory determination of CTMax and associated stress physiology

Study fish were captured from local tidal creeks using seine nets deployed at creek mouths to intercept bonefish on incoming or outgoing tides between February 17, 2007 and March 16, 2007. Fish were transported to the research facility using the methods outlined in Murchie et al. (2009) and held in large (3.7 m diameter × 1.25 m deep; 13,180 L) circular tanks housed in a covered, open-sided outdoor facility. Tanks were continuously supplied with fresh seawater (1800 L h^{-1}) at ambient temperatures, and were maintained under a natural photoperiod. Fish were fed a diet of queen conch (*Eustrombus gigas*) offal and/or commercially available sinking pellets (6 mm, Skretting, Canada; 13 mm, Zeigler, USA). Test fish, however, were not fed 24 h prior to or during experimental trials (see Fangue and Bennett, 2003).

The CTMax of bonefish was determined at two different seasonal acclimation temperatures, one representative of late spring (27.3 ± 1.3 °C; mean ± SD) and one of summer (30.2 ± 1.4 °C; mean ± SD) temperatures. The 'late spring' sampling period occurred between May 2 and 17, 2007, and the 'summer' sampling period occurred from August 6 to 23, 2007. The use of fluctuating acclimation temperatures representative of natural conditions, rather than constant acclimation temperatures, is an alternative approach to investigating thermal tolerances of fishes (see Currie et al., 2004). At 24 h prior to experimentation, bonefish were netted from the large circular holding tanks and placed in individual darkened flow-through tanks (approximately 100 L) to minimize exercise and stress associated with tank capture (Suski et al., 2007). Individual flow-through tanks were also continuously supplied with fresh seawater at ambient conditions. A maximum of three bonefish were placed in individual flow-through tanks at a time in preparation for CTMax determinations the next day. Temperature data loggers (Hobo-H8 temperature logger, Onset Computer Corporation, ± 0.7 °C accuracy) encased in waterproof housings were used to measure acclimation temperatures within the tanks. During experimentation, an individual was removed from its flow-through tank and quickly (< 30 s) transferred to an aerated thermal bath (142 L insulated cooler). Starting temperatures within the thermal bath were consistent with conditions in the individual's flow-through tank immediately prior to transfer. Water temperature within the bath was raised by 0.2 °C min^{-1} using two submersible heaters (Model 306, Heet-O-matic, Cole Parmer, Newark, NJ), until the fish lost equilibrium for one minute (Beitinger et al., 2000; Fangue and Bennett, 2003). Following sustained equilibrium loss, the water temperature was recorded and the fish was removed for blood sampling and subsequent determination of secondary indicators of stress. Individuals were restrained by hand in a supine position (without the use of anesthetic) in a foam-lined trough filled with seawater, at a depth to completely submerge their gills. Using a 21 gauge needle, approximately 1.5 mL of blood was drawn from the caudal vasculature into a 3 mL lithium heparinized vacutainer (BD vacutainer blood collection tube; Becton, Dickinson and Company; Franklin Lakes, NJ). After phlebotomy (typically less than 45 s), the blood sample was held in an ice-water slurry until sample processing, storage and analysis as described below. The total length of the bonefish was recorded to the nearest mm, and fish

were returned to original holding tanks with conspecifics. To generate control (resting) physiological values for comparative purposes, the above process was repeated without the thermal trial for at least eight bonefish at each acclimation temperature. Trials were conducted between 0700 and 2200 h dependent on when fish were placed in individual flow-through tanks, and the number of bonefish prepared for experimentation that day. CTMax was calculated as the arithmetic mean of the temperatures at which the fish lost equilibrium (Beitinger et al., 2000).

2.2. Effects of multiple stressors

Because stressors rarely act independently in the natural environment, we conducted an experiment to examine the combined effects of thermal stress and capture/holding stress. Bonefish were seined in tidal creeks on an outgoing tide and sampled for blood after being held in a pen (1.3 m × 0.8 m × 1.25 m deep, 3.1 cm extruded plastic mesh) for either a short (6 min or less) or long (7–15 min) duration. The experiment was conducted at two distinct water temperatures; 22 °C (February 17–23, 2007) and 32 °C (August 28, 2008). Following blood sample collection, glucose and lactate levels were quantified on whole blood using commercially available handheld devices (ACCU-CHECK glucose meter, Roche Diagnostics, Basel, Switzerland and Lactate Pro LT-1710 portable lactate analyzer, Arkray Inc., Kyoto, Japan) previously validated for use on bonefish (see Cooke et al., 2008). An i-STAT point of care device (Heska Corporation, Fort Collins, CO, USA) was used to measure Na$^+$, K$^+$, and Cl$^-$ values for fish in the CTMax trials, whereas plasma samples from the field assessment of multiple stressors were analyzed by an accredited animal science diagnostics lab (Vita-Tech, Markham, Ontario, Canada) using a Roche-Hitachi Analyzer (Roche Diagnostics, Basel, Switzerland). Additionally, hematocrit values were assessed by spinning whole blood samples in a centrifuge (Clay Adams Compact II Centrifuge) at 10 000g for 5 min to separate plasma from red cells, and by then measuring the ratio with a ruler. To allow for comparison of ion values determined for fish in the CTMax trials with those determined for fish in the field assessment of multiple stressors, values obtained via the i-STAT were converted to 'gold standard' laboratory values using predictive equations derived from Cooke et al. (2008).

2.3. Linking spatial ecology with thermal regimes in tidal creeks and coastal areas

2.3.1. Collection of ambient water temperature data

A total of eight temperature data loggers were deployed in the mouths (1.2 m deep) and upper reaches (0.3 m deep) of three tidal creeks (Page Creek, Kemps Creek, and Broad Creek, which has two mouths), plus one open coastline location just off CEI (2.5 m deep) (Fig. 1). Temperature loggers were deployed in Broad and Kemps Creek in October 2004, and in Page Creek and off CEI in May 2006 by affixing them to a cinder block with twine. Hourly temperatures were recorded at the water–substrate interface. For the purpose of this study, data collected from the temperature loggers between the date of deployment and December 31, 2007 were used.

2.3.2. Spatial ecology of bonefish

Between November 1, 2005 and March 16, 2007, 47 adult bonefish (495 ± 45 mm total length; mean ± SD) were captured with seine nets (as described above) and were implanted with acoustic transmitters (model V13 coded tags, 13 mm diameter, 36 mm long, 6 g, 700 day battery life, Vemco Inc., Shad Bay, NS.). Bonefish were anesthetized with MS-222 (approx. 100 ppm) prior to surgery and then placed on a surgery table where fish gills were supplied with a maintenance dose of MS-222 (approx. 50 ppm)

in fresh seawater. To implant the transmitter, a small incision (2–3 cm) was made to one side of the ventral midline, posterior to the pectoral fins. The transmitter was inserted and gently guided towards the pectoral fins. The incision was closed with 3–4 simple interrupted sutures (Ethicon 3-0 PDS II monofilament absorbable suture material, Johnson and Johnson, New Jersey). The total length of the fish (mm) was measured and recorded. The entire procedure took less than 5 min. Prior to release, bonefish were held for up to 1 h in flow-through holding pens (1.3 m × 0.8 m × 1.25 m deep, 3.1 cm extruded plastic mesh).

Movements of tagged bonefish were monitored through the use of a 27 hydroacoustic receiver array (VR2 and VR2W receivers, Vemco Inc., Shad Bay, NS). The array covered points along a 23 km stretch of coastline, with receivers strategically deployed at choke points (e.g., creek mouths) or as curtains extending up to 1.5 km perpendicular to the shoreline (Fig. 1). Location of seven of the receivers corresponded closely to the locations of temperature loggers within the three tidal creeks (Page Creek, Kemps Creek, and Broad Creek) (Fig. 1). Individual receivers were secured to a short piece of rebar anchored into a concrete block. Receivers were positioned vertically in the water column at depths greater than 1 m deep at low tide, and were positioned either horizontally or 5–10° above horizontal in water less than 1 m deep at low tide. Range tests determined that receivers located in water greater than 1 m had a radius coverage of 250 m, whereas receivers in shallow water (<1 m) had a radius coverage of as little as 30 m, due to shoreline confinement. 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 (e.g., creek mouths), such that data correction for receiver range was not required. Wind and wave conditions as well as water depth and tidal cycles influenced the detection range of individual receivers (Heupel et al., 2006). Even at slack low tides, all of the receivers were covered by at least 20 cm of water and had the potential to be accessed by the tagged fish. The hydrophones were deployed between November 2, 2005 and May 19, 2007 and were visited regularly for downloading and cleaning. For the purpose of this study, the last download period included data up to December 31, 2007.

2.4. Data analysis

All statistical analyses on collected and derived data were completed using JMP 7.0.2 (SAS Institute, Cary, NC). 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). For laboratory determination of CTMax and associated stress physiology, a one-way analysis of variance (ANOVA) was used to determine if there were any size (total length) differences in bonefish within and between treatment groups (i.e., CTMax or control) and acclimation temperatures (i.e., 27.3 or 30.2 °C). A two-sample t-test was used to compare laboratory determined CTMax values between the two acclimation temperatures. A two-way ANOVA, with main effects of acclimation temperature and treatment, was used to compare blood chemistry values and to determine the level of stress associated with reaching the CTMax. The effects of temperature and duration of holding stress from the field trial were also evaluated using a two-way ANOVA.

To link the spatial ecology of bonefish to the thermal regimes in the three tidal creeks where temperature data loggers were deployed, detections recorded within the hydrophone array between June and December 2007 were examined. This time period was selected to: (1) exclude periods where movements included forays to offshore locales, which we hypothesize indicate spawning activity (Murchie and Danylchuk, CEI, unpublished

data); (2) maximize the number of possible bonefish at large; and (3) maximize the number of receivers for which bonefish could be detected at, since all 27 receivers had been deployed by May 19, 2007. Receivers were classified as being in one of three habitat types; creek backwaters (receivers #6, #12, and #19), creek mouths (receivers #5, #11, #16, #18, and #27), and open coastline (remaining receivers) (Fig. 1). The total number of detections of each bonefish picked up in the array was broken down into months (i.e., June to December) and habitat types. The total number of detections for each fish in each habitat type was divided by the total number of detections of the fish for that month and multiplied by 100 to give a percentage. Percentages were tallied across each habitat type for each month and divided by the total number of bonefish at large during the June to December 2007 period and further divided by the number of receivers in each habitat (due to the uneven number of receivers per habitat). A repeated measures two-way ANOVA followed by a Tukey–Kramer HSD test (Day and Quinn, 1989) was used to determine whether month or habitat influenced the percentage of detections of bonefish. Within the June to December 2007 time period, all detections within creek backwaters were further examined. For each individual bonefish detected in creek backwaters their proportion of detections was calculated for each maximum water temperature. The relationship between the proportion of detections of bonefish in the backwaters of the tidal creeks and the maximum daily water temperature recorded was evaluated with a simple linear regression model. Proportional data were arcsine root transformed and plotted against maximum water temperatures. When bonefish were detected on days when water temperatures approached or exceeded CTMax values, further examination of the data was conducted to determine the exact water temperature at the time of bonefish detection.

3. Results

3.1. Laboratory determination of CTMax and associated stress physiology

A total of 39 wild adult bonefish (438 ± 34 mm total length; mean $\pm$ SD) were captured from local tidal creeks and relocated to the CEI seawater research facility for acclimation and subsequent thermal tolerance testing or use as controls (Table 1). There was no significant difference between the size of bonefish within and between treatment groups from the two acclimation temperatures ($F=2.65$, $p=0.064$). The CTMax values of 36.4 ± 0.5 and 37.9 ± 0.5 °C for bonefish acclimated to 27.3 and 30.2 °C, respectively (Table 1), were significantly different between acclimation temperatures ($t=7.22$, $p<0.0001$). Blood chemistry values after reaching CTMax were significantly different between controls and CTMax fish for all parameters except chloride (Fig. 2, Table 2). Acclimation temperature was a significant main effect for all parameters, and no interaction between treatment and acclimation temperature was detected (Table 2). More specifically, concentrations of K^+, lactate, and glucose increased relative to control values following CTMax trials for both acclimation temperatures. In addition, acclimation of bonefish to either 27.3 or 30.2 °C had significant impact on the level of change among physiological parameters following CTMax trials. The accumulation of lactate as well as plasma glucose for bonefish acclimated to 30.2 °C was significantly higher than that for bonefish acclimated to 27.3 °C.

3.2. Effects of multiple stressors

When bonefish were exposed to an additional stressor (i.e., handling), fish tended to exhibit the most severe physiological

Table 1
Summary statistics of bonefish size, CTMax, and blood chemistry results from the CTMax trials at two acclimation temperatures. Values are means $\pm$ SD for CTMax and means $\pm$ SE for blood chemistry.

Acclimation temperature (°C)	Treatment	n	Total length (mm)	CTMax (°C)	Lactate (mmol/L)	Glucose (mmol/L)	Na$^+$ (mmol/L)	K$^+$ (mmol/L)	Cl$^-$ (mmol/L)
27.3 $\pm$ 1.3	CTMax	10	428 $\pm$ 30	36.4 $\pm$ 0.5	9.2 $\pm$ 0.9[a]	8.1 $\pm$ 0.8[a]	171.0 $\pm$ 1.6[a]	11.4 $\pm$ 0.9[a]	168.8 $\pm$ 1.0[a]
	Control	11	422 $\pm$ 31		2.9 $\pm$ 1.0	5.2 $\pm$ 0.4	178.8 $\pm$ 3.5	7.9 $\pm$ 0.7	167.5 $\pm$ 1.0[b]
30.2 $\pm$ 1.4	CTMax	10	455 $\pm$ 29	37.9 $\pm$ 0.5	9.9 $\pm$ 0.8	11.7 $\pm$ 1.7	182.2 $\pm$ 2.7[a]	9.7 $\pm$ 0.6[a]	173.8 $\pm$ 1.0[a]
	Control	8	453 $\pm$ 40		5.9 $\pm$ 0.8	6.5 $\pm$ 0.5	194.4 $\pm$ 8.7[c]	6.6 $\pm$ 0.6[c]	180.9 $\pm$ 7.6[c]

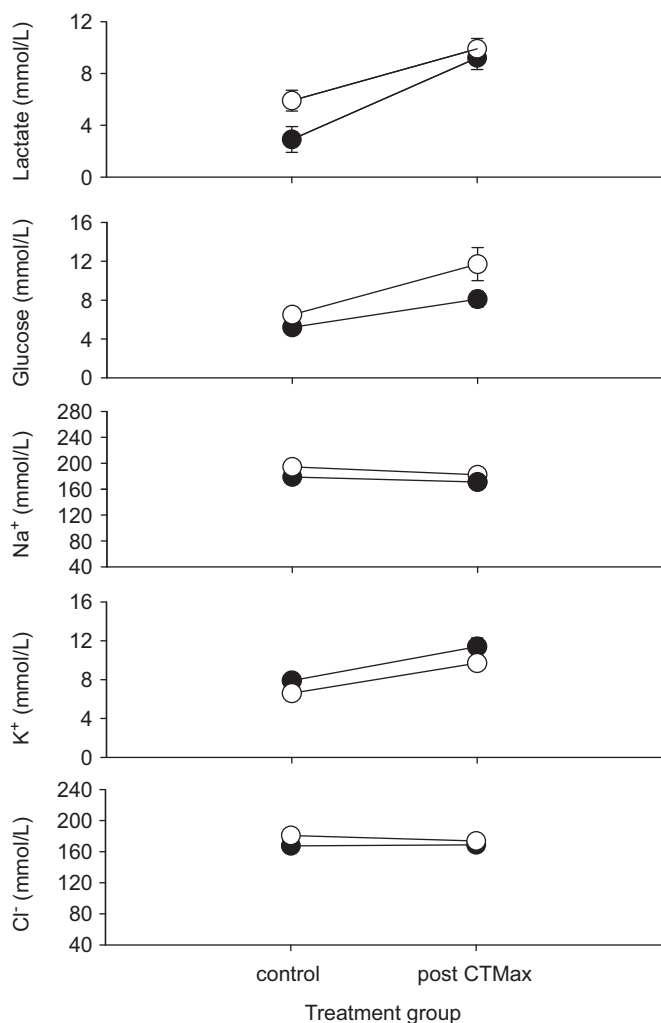[a] $n = 9$.
[b] $n = 8$.
[c] $n = 7$.

Fig. 2. Blood chemistry values for bonefish exposed to thermal stress (CTMax) compared to controls. Solid circles represent acclimation to 27.3 °C, whereas open circles represent acclimation to 30.2 °C. Error bars represent standard error. Results for a two-way ANOVA of the data are presented in Table 2.

stress response at the highest water temperature (Fig. 3, Table 3). Indeed, for all parameters except potassium, temperature was the significant main effect (Table 4). Lactate values ranged from as low as 3.7 mmol/L to as high as 14 mmol/L. Recorded values for glucose ranged from 3.4 to 10.8 mmol/L. Hematocrit values ranged from 0.21 to 0.64. Ion values ranged from 63.83 to 238.00, 1.42 to 11.37, and 149.00 to 226.00 mmol/L for sodium, potassium, and chloride, respectively. The duration of holding was significant for lactate, glucose, hematocrit, and sodium, but not for potassium or chloride

(Table 4). An interaction between temperature and the duration of stressor existed for lactate (Table 4).

3.3. Linking spatial ecology with thermal regimes in tidal creeks and coastal areas

Hourly water temperatures collected within the tidal creeks peaked at 40.6 °C in the backwaters of Kemps Creek in June 2007 and reached a low of 9.03 °C in January of 2005 in the same location. Daily fluctuations of up to 11.40 °C were recorded at the mouth of Kemps Creek on May 28, 2006. Temperatures varied the most within the backwaters and mouths of tidal creeks, but were much more stable at offshore locations (Fig. 4).

Bonefish implanted with transmitters in August of 2006 suffered a high percentage of mortality compared to fish implanted in February or March of 2007. During the two days in which surgeries were conducted in August 2006, the mean water temperature at the mouth of the creek was 29 °C. Out of the 21 fish tagged at 29 °C, 14% were suspected to be dead within 48 h, and 57% within one week, as evidenced by the lack of detection at any receivers as of December 31, 2007. Presumptive mortality rates were much lower when bonefish were implanted in cooler (20–23 °C) waters during February and March of 2007, with 4% and 12% mortality after 48 h and one week, respectively. Of the surviving bonefish, ten were picked up frequently within the hydrophone array between June and December 2007, logging 92,671 detections.

The highest percentage of detections between June and December 2007 were at receivers located in the creek mouths, followed by those in the open ocean, and backwater portions of creeks ($F = 26.46$, $p < 0.0001$) (Fig. 5). Month was not a significant main effect in the model ($F = 0.18$, $p = 0.981$), and no significant interaction between month and habitat type occurred ($F = 0.92$, $p = 0.531$). A significant positive relationship was determined between the arcsine root transformed proportion of detections in the backwaters of the creeks and water temperatures ($r^2 = 0.09$, $F = 33.19$, $p < 0.0001$) (Fig. 6). When maximum daily temperatures exceeded the conservative CTMax of 36.4 °C, all detections of bonefish in the backwaters of tidal creeks were examined further to determine the exact times at which the fish were detected at the receiver and the hourly maximum temperature recorded. Although one bonefish was detected on June 25, 2007 when the daily maximum temperature in the backwaters of Kemps Creek reached 37.88 °C, the maximum temperature recorded while the bonefish was detected 23 times between 6:16 and 8:03 was 29.5 °C. Maximum water temperatures approached the CTMax on June 21, 2007 at 36.13 °C. On this day, two bonefish were detected in the backwaters of Broad Creek, between 13:10 and 14:33, when hourly water temperatures of 33.17 and 34.01 °C were recorded at 13:00 and 14:00, respectively. Additionally, one bonefish was detected in the backwaters of Kemps Creek on June 21 between the hours of 14:16

Table 2
Two-way ANOVA results for blood chemistry values following the laboratory determination of CTMax for bonefish. All significant values are designated with an asterisk.

Response variable	Factor	n	SS	F	P
Lactate	Treatment	38	251.368	31.975	< 0.0001[*]
	Acclimation temperature		34.002	4.325	0.045[*]
	Treatment × Acclimation temperature		12.718	1.618	0.212
Glucose	Treatment	38	155.341	15.548	0.0004[*]
	Acclimation temperature		57.254	5.731	0.022[*]
	Treatment × Acclimation temperature		11.703	1.171	0.287
Na^+	Treatment	36	879.508	5.341	0.027[*]
	Acclimation temperature		1580.562	9.599	0.004[*]
	Treatment × Acclimation temperature		43.134	0.262	0.612
K^+	Treatment	36	95.535	20.405	< 0.0001[*]
	Acclimation temperature		20.540	4.387	0.044[*]
	Treatment × Acclimation temperature		0.580	0.124	0.727
Cl^-	Treatment	33	68.477	0.766	0.389
	Acclimation temperature		686.416	7.680	0.010[*]
	Treatment × Acclimation temperature		147.055	1.645	0.210

and 14:27 and 18:00 to 18:15, with hourly temperatures of 32.32 and 32.76 °C, respectively.

To further examine the range of temperatures to which bonefish are exposed to on a daily basis, a thermal trace for a 72 h period in August and January was constructed for one individual bonefish by matching the hourly temperature recorded by the temperature logger at the corresponding receiver (Fig. 7). For all receivers outside the creeks, the temperature recorded by the logger on the coastline off of CEI was used. The traces constructed are representative of other bonefish activity as another tagged bonefish was found schooling with this individual during the same August time period the temperature trace was constructed. The range of water temperatures measured within the 72 h trace was 5 °C in the summer and 3 °C in the winter.

4. Discussion

This study represents the first effort to quantify the thermal tolerance and environmental relations of bonefish. The laboratory-determined CTMax of bonefish, 36.4 ± 0.5, and 37.9 ± 0.5 °C for individuals acclimated to 27.3 ± 1.3 and 30.2 ± 1.4 °C, respectively, typically exceeds daily maximum temperatures observed in the tidal creeks. Observed thermal tolerances for bonefish are not remarkable when compared to 22 species of freshwater fish found in North America that exhibit CTMax values of 40 °C or higher (see Beitinger et al., 2000). For example, largemouth bass (*Micropterus salmoides*) acclimated at 28 °C attained a CTMax of 40.1 °C (Smith and Scott, 1975). Although limited data exist for tropical marine species (Kimball et al., 2004), there are a few studies with which comparisons can be made. For 15 species of reef fish acclimated to 26.5 ± 0.5 °C, CTMax values ranged between 34.7 and 40.8 °C, with the least tolerant species exhibiting a CTMax 8 °C above mean sea temperatures in the tropical eastern Pacific (Mora and Ospina, 2001). Atlantic stingrays (*Dasyatis sabina*), which inhabit shallow bays prone to rapid temperature changes, had CTMax values of 39.3 and 43.2 °C when acclimated to 20.5 or 35.1 °C, respectively (Fangue and Bennett, 2003). A combination of physiological tolerance and behavioral adaptation may be responsible for allowing bonefish to exploit the backwaters of tidal creeks when temperatures peak. Indeed such a combination has been suggested as the mechanism allowing fish species to occupy hyperthermal rockpools in the Dry Tortugas, even though water temperatures often meet or exceed thermal tolerances (Fangue et al., 2001).

Reaching the CTMax for bonefish induced physiological changes as evidenced by observed changes in blood chemistry. Elevations in

blood lactate, glucose, Na^+, and K^+ were observed for bonefish exposed to temperatures at their CTMax relative to controls. Exposure to multiple stressors (i.e., capture/holding stress combined with increased ambient water temperatures) further exacerbated the response in blood lactate, glucose, hematocrit, and several ions (Na^+ and Cl^-). In fact, recorded values of lactate, glucose, and hematocrit for bonefish in field trials at the highest water temperature exceeded those documented in moribund fish following transport and handling at 21–24 °C (Murchie et al., 2009), suggesting that fish in these experiments underwent severe physiological disturbance. Results documented in this study are consistent with the response of bonefish exposed to acute stressors such as exercise (Suski et al., 2007) and confinement stress (Cooke et al., 2008), and recorded values are within the realm of those determined for other marine species (e.g., coral trout, *Plectropomus leopardus* (Frisch and Anderson, 2000); coho salmon, *Onchorhynchus kisutch* (Farell et al., 2001); sockeye salmon, *O. nerka* (Cooke et al., 2006a); ling cod, *Ophiodon longatus* (Milston et al., 2006)). Lactate production occurs in white muscle in response to conditions of strenuous exercise and hypoxia (Driedzic and Kiceniuk, 1976). In this study, activity in the thermal bath increased as bonefish approached their CTMax. Individuals attempted to escape confinement by increasing their swimming activity, and many jumped against the lid. Despite aerating the CTMax apparatus, dissolved oxygen levels did decrease slightly with rising water temperatures and oxygen consumption by the bonefish. Near the highest water temperatures, dissolved oxygen did approach hypoxic levels (i.e. < 5 mg/L; Suski, University of Illinois, unpublished data). Our field observations suggest that dissolved oxygen in the wild also decreases as waters in tidal creeks approach their maximal temperatures (Cooke, Carleton University, unpublished data). As such, this decrease in dissolved oxygen that parallels the increase in water temperature during the CTMax studies is representative of what fish would likely experience in the wild. Increased glucose levels (i.e., hyperglycemia) indicate the release of glucose into the bloodstream to fuel increased muscular activity, and the increase in passive ion influxes is consistent with the loss of water in marine fish during a stress response (Wendelaar Bonga, 1997).

Observations of increased stress in captured bonefish at high water temperatures have implications for activities such as catch-and-release angling. Elevated water temperature has repeatedly been identified as a contributing factor to mortality associated with angling (see Muoneke and Childress, 1994; Thorstad et al., 2003). Danylchuk et al. (2007) found that although the susceptibility of bonefish to post-release predation was not directly related to water

temperature, bonefish spent more time resting following release at higher water temperatures. It is likely that the higher water temperatures associated with our tagging efforts in August played

Fig. 3. Blood chemistry values for bonefish exposed to multiple stressors (i.e., temperature and holding). Duration of stress was either short (6 min or less) or long (7–15 min). Solid circles represent trials conducted at 22 °C and open circles at 32 °C. Error bars represent standard error. Results for a two-way ANOVA of the data are presented in Table 4.

a role in the loss of some transmitter-implanted fish. Surgical error associated with the implantation procedure itself is rare and unlikely, so most surgery-related mortality is likely to be a result of the cumulative stress of handling and post-operative stress rather than surgical injury *per se* Wagner and Cooke (2005).

Linkages between the spatial ecology of bonefish and its thermal habitat were accomplished through the use of telemetry coupled with temperature loggers along the coast and in the mouths and upper portions of tidal creeks. Bonefish were found to spend more time at creek mouths than coastal open ocean or backwater habitats. This can be expected as creek mouths are linkages between the ocean and backwater habitats. As water temperatures in backwater areas increased, the proportion of detections in the backwater stretches of creeks increased. Such a response is consistent with the need for more food energy to fuel increased metabolic costs associated with higher water temperature (Hochachka and Somero, 1973). Bonefish were not found in tidal creeks when maximum temperatures exceeded their determined CTMax, but they were still using the creeks at 34.01 °C. During a post-release behavior experiment conducted in Broad and Kemps Creek, Danylchuk et al. (2007) captured bonefish in water with temperatures exceeding 35 °C. This is the highest known water temperature recorded when bonefish were present in tidal creeks.

Only two other known studies have attempted to relate bonefish movement to water temperatures. Colton and Alevizon (1983) monitored three individual bonefish for 32 h total, spread over a 100 day period. During each manual tracking event, water temperature was recorded at approximately 30 min intervals. The maximum range of water temperature measured during a single tracking event was 8 °C (24–32 °C). In this study, a range of 5 °C was found for a bonefish over a 72 h period in the summer and 3 °C over a 72 h period in the winter. In the study by Humston et al. (2005), bonefish movements, as determined by an acoustic telemetry array, were related to daily mean and/or maximum air temperatures. Only two of their study fish were detected for a sufficient period (40–61 d) for analyses, and only one of the fish demonstrated some variation in movements that could be related to air temperature. The authors observed that the individual fish retreated to deeper waters with abrupt increases in air temperature and back to shallower waters when air temperatures decreased. Both studies inferred the use of deep channels as refugia when water temperatures increased. The use of behavioral thermoregulation may explain how bonefish in this study were able to withstand water temperatures approaching their CTMax. Future work using physiological telemetry where the tags carried by the fish transmit water temperature information in addition to fish identification, date, and time is suggested for achieving the most accurate assessment of thermal habitat selection by bonefish. This will also provide insight into the temperatures in which individuals are acclimatized to the prior to making forays into warmer waters. Additional studies, which should include an assessment of maximum and minimum acclimation temperatures as well as CTMax and critical thermal minimum across the acclimation range, would be beneficial so that a thermal tolerance polygon (see Fangue and Bennett, 2003) can be constructed for bonefish and their optimal
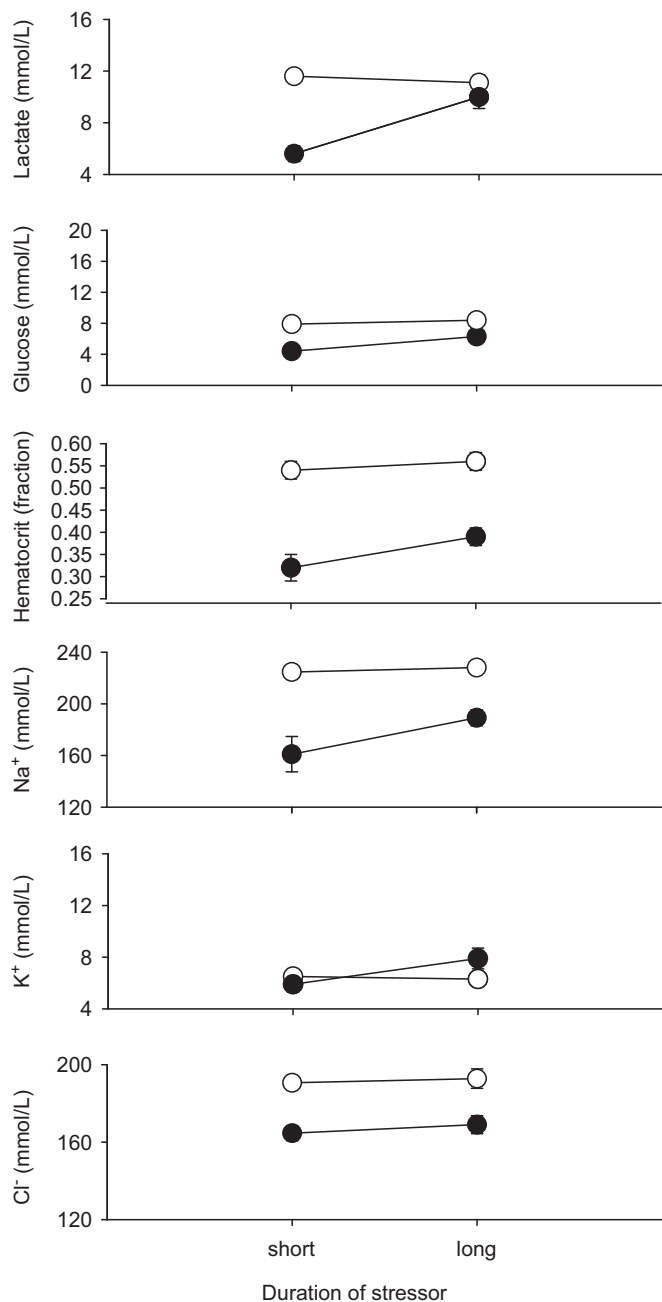
Table 3
Summary statistics of blood chemistry results from the field trials examining the effects of multiple stressors (temperature and handling stress) on bonefish. Values are means ± SE.

Temperature (°C)	Duration of stressor	n	Lactate (mmol/L)	Glucose (mmol/L)	Hematocrit (fraction)	Na$^+$ (mmol/L)	K$^+$ (mmol/L)	Cl$^-$ (mmol/L)
22	Short	9	5.6 ± 0.6	4.4 ± 0.3	0.32 ± 0.03	161.0 ± 13.7	5.9 ± 0.6	164.6 ± 3.8
	Long	8	10.0 ± 0.9	6.3 ± 0.5	0.39 ± 0.02	189.2 ± 6.2	7.9 ± 0.8	169.0 ± 4.6
32	Short	9	11.6 ± 0.3	7.9 ± 0.5	0.54 ± 0.02	224.6 ± 1.6	6.5 ± 0.3	190.6 ± 1.2
	Long	12	11.1 ± 0.6	8.4 ± 0.4	0.56 ± 0.02	228.0 ± 4.4	6.3 ± 0.5	192.8 ± 5.0

Table 4
Two-way ANOVA results for blood chemistry values following field trials examining the effects of multiple stressors (temperature and handling stress) on bonefish. All significant values are designated with an asterisk.

| Response variable	Factor	n	SS	F	P
Lactate	Temperature	38	117.402	28.930	< 0.0001*
	Duration of stressor		35.755	8.811	0.006*
	Temperature × Duration of stressor		55.040	13.563	0.0008*
Glucose	Temperature	38	72.259	41.720	< 0.0001*
	Duration of stressor		13.009	7.511	0.010*
	Temperature × Duration of stressor		3.993	2.305	0.138
Hematocrit	Temperature	37	0.344	83.553	< 0.0001*
	Duration of stressor		0.017	4.241	0.047*
	Temperature × Duration of stressor		0.009	2.152	0.152
Na$^+$	Temperature	38	24,316.498	44.634	< 0.0001*
	Duration of stressor		2329.408	4.276	0.046*
	Temperature × Duration of stressor		1426.215	2.618	0.115
K$^+$	Temperature	38	2.579	0.850	0.363
	Duration of stressor		6.879	2.267	0.141
	Temperature × Duration of stressor		10.123	3.336	0.077
Cl$^-$	Temperature	28	3175.319	20.910	0.0001*
	Duration of stressor		57.143	0.376	0.545
	Temperature × Duration of stressor		6.671	0.044	0.836
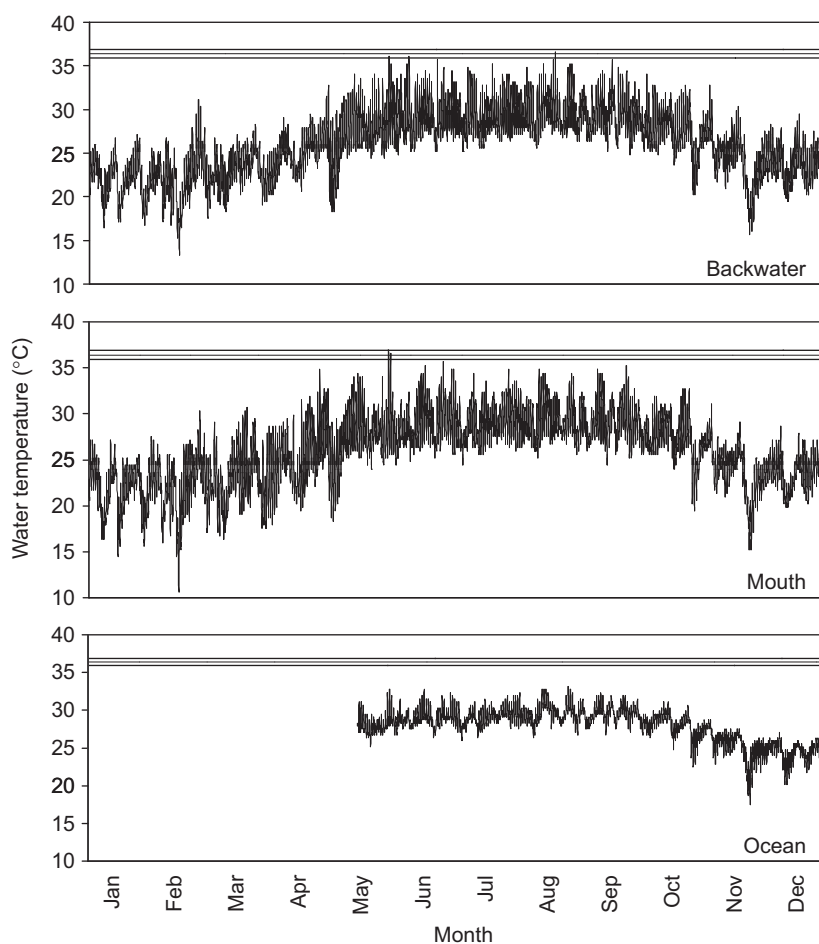
Fig. 4. Representative sample of hourly temperature data collected from the backwaters and mouths of tidal creeks, along with data from an offshore data logger. The upper panel is data from the backwaters of Kemps Creek, the middle panel is data from the mouth of Kemps Creek, and lower panel is data from offshore of CEI, between January 1 and December 31, 2006. The solid horizontal line provides a point of reference of the lowest determined CTMax of bonefish (i.e., 36.4 °C), and the dashed lines represent the upper and lower SD.

temperature determined, since aerobic scope, cardiovascular function and growth peak at optimal temperatures (Wood and McDonald, 1997).

Given the importance of tidal creeks as bonefish habitat, it is worth considering potential changes in thermal habitat availability under future climate change scenarios. The Intergovernmental Panel on Climate Change (IPCC) predicts an increase in water temperature of 1.8 or 3.4 °C per 100 years for atmospheric carbon dioxide concentrations of 550 and 800 ppm by the year 2100, respectively (IPCC, 2001). Given that the future impacts of climate
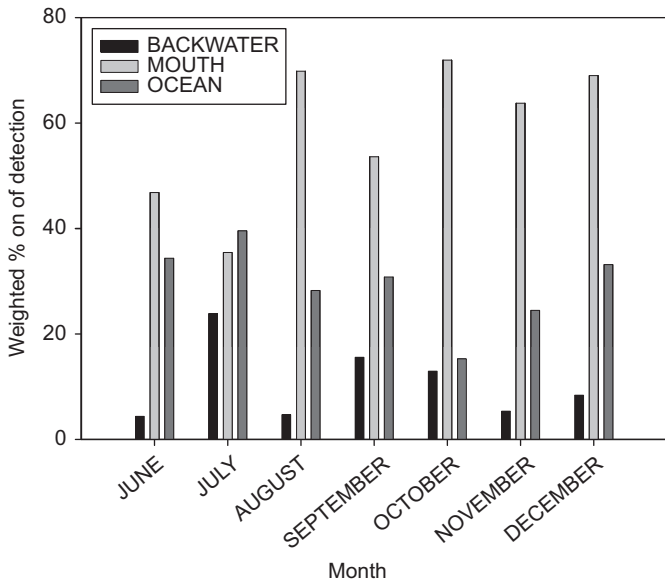
Fig. 5. Weighted percentage of detections of tagged bonefish in various habitat types between June and December 2007. A description of the weighting procedure is provided in the methods.
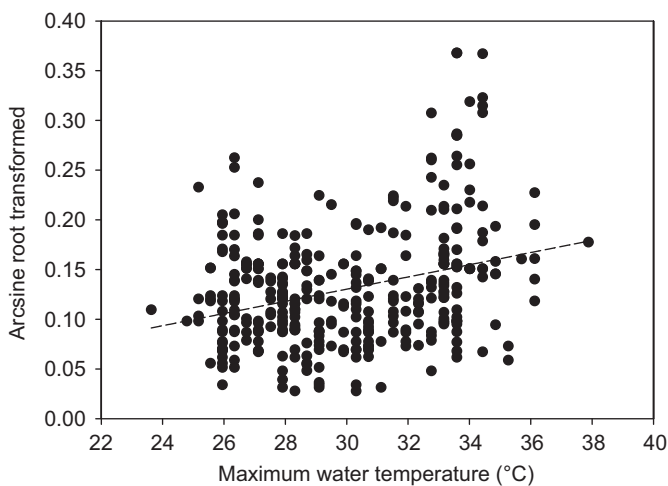

Fig. 6. Scatterplot of arcsine transformed proportions of bonefish detections ($n=338$) in tidal creek backwaters between June and December 2007 versus maximum daily water temperatures. The resultant model was arcsine root proportion of detections$=-0.054+0.006$ maximum water temperature ($r^2=0.090$, $F=33.19$, $p<0.0001$).
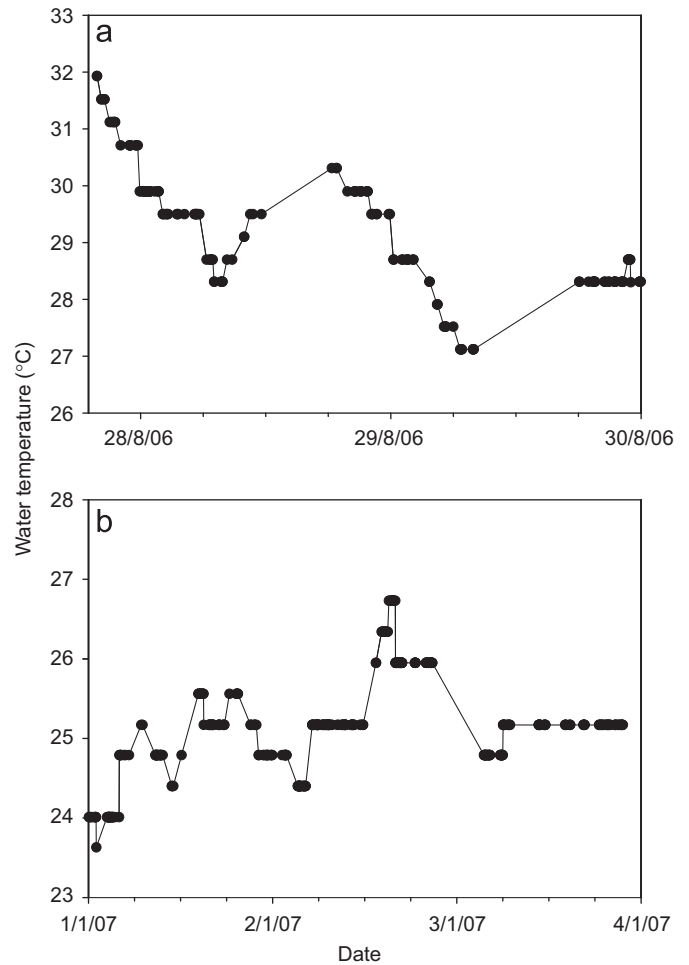

Fig. 7. Corresponding water temperatures recorded over a 72 h period for each detection of an individual bonefish in August 2006 (panel a) and January 2007 (panel b). Dates are given as dd/mm/yy.

change for the Bahamas are based on IPCC predictions (BEST, 2002), and that IPCC predictions are in-line with historical data for the region (BEST, 2001), examination of tidal creek temperatures under present conditions and predicted scenarios can be compared to determine the percentage of time water temperatures exceed the CTMax of bonefish. Similar approaches have been used for other ecosystems in the tropics (e.g., coral reefs; Hoegh-Guldberg et al., 2007) to predict the effects of global warming. By using water temperature data collected from January 1 to December 31, 2006 from the upper portion of Kemps Creek, where the majority of bonefish detections were logged for backwater stretches, current conditions found water temperatures exceeded the conservative CTMax of 36.4 °C 0.27% of the time. Under Scenario 1, an increase in 1.8 °C, water temperatures are predicted to exceed CTMax 4.66% of the time. Under Scenario 2, an increase of 3.4 °C, temperatures are predicted to exceed CTMax 18.90% of the time. Although there is

capacity for individual bonefish to acclimate to changes in seawater temperatures over time, it is possible that populations as a whole will be less tolerant. For example, Pörtner and Knust (2007) observed a strong negative correlation between estimated eelpout (*Zoarces viviparous*) population sizes and summer water temperatures, suggesting that the temperatures causing population declines are lower than critical tolerances. Physiological limitations of cardiac function in waters with elevated temperatures, and thus diminished dissolved oxygen levels, are likely to limit the aerobic scope. By limiting aerobic scope, foraging efficiency is decreased and individuals are more prone to predation (Wang and Overgaard, 2007; Pörtner and Farrell, 2008). In turn, the overall energy budget of the fish is affected, potentially influencing immune function, reproduction, and growth (Barton and Iwama, 1991; Somero, 2002). A more accurate assessment of the potential performance of bonefish in light of climate change can only be possible, however, with more experimental studies and long-term monitoring of populations.

Collectively, the data from our laboratory and field studies suggest that bonefish occupy habitats that approach their laboratory-determined CTMax and can apparently do so without significant sub-lethal physiological consequences or mortality, except when exposed to additional stressors. Given that human interactions with fish continue to increase in coastal and estuarine habitats (Turner et al., 1996), the potential for more frequent interaction between fish and humans (e.g., general disturbance, Ellison and Farnsworth, 1996; recreational

fishing, Cooke et al., 2006b), as well as general changes in habitat quality (Ellison and Farnsworth, 1996; Turner et al., 1996) could make fish that use tropical tidal creeks particularly vulnerable to climate change. Moreover, climate change has the potential to reduce the availability of upper creek habitats that appear to be important for feeding and predator avoidance (Colton and Alevizon, 1983). Additional research is required to understand the energetic tradeoffs associated with occupying dynamic thermal habitats and how climate change will influence the distribution and condition of a variety of marine fish species that reside in tropical tidal flats (Perry et al., 2005). It is also important to understand how temperature influences the response of fish to hypoxia and salinity fluctuations, two critical environmental variables that will undoubtedly change with warming temperatures (Harley et al., 2006). We advocate for future studies that integrate laboratory and field data to understand how animals adapt to dynamic environments and to understand how they will be influenced by human activity and environmental change (Wikelski and Cooke, 2006; Pörtner and Farrell, 2008).

Acknowledgments

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