Thermal biology and swimming energetics of bonefish (*Albula vulpes*) in Eleuthera, The Bahamas.

By

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ABSTRACT

Knowledge of the swimming energetics and thermal biology of bonefish is extremely limited, yet this information is critical to understanding the thermal windows for tropical intertidal species, quantifying fish fitness in relation to temperature and understanding the potential future effects of climate change. To address this gap in knowledge a combination of laboratory and field approaches were used to study the thermal biology of bonefish (*Albula vulpes*). The critical swimming speed (U_{crit}), metabolic rates (MO_{2max} and $MO_{2routine}$), scope for activity, and cost of transport (COT_{net}) was assessed across a range of temperatures for bonefish in The Bahamas, 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} (i.e., 96cm/s) was 28°C and the optimal temperature for scope for activity (i.e., 7.5mgO_2/min/kg) was 26.7°C. The thermal profile of wild bonefish was also determined by surgically implanting iButton thermal loggers into the fish and recapturing those fish after they had been at liberty. Of the 138 implanted fish, 8 were recaptured with functional iButtons. Their thermal profiles revealed that bonefish did not exceed laboratory-determined critical temperatures (i.e., 14.5°C and 38°C) and spent the majority of their time at their optimal temperatures. Nonetheless, fish experienced wide variation in daily thermal experience – both through time and among individuals. Overall, this research yields a better understanding of bonefish thermal biology, and the potential impacts of climate change, as well as paves the way for creating a complete bioenergetics model for the species.

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1.0 INTRODUCTION

1.1 Water Temperature and Climate Change

Water temperature is the “master” environmental factor influencing the biology of fish (Brett 1971). Water temperature exerts more control over fish than any other single abiotic factor as it influences all biochemical, physiological, and life history activities. Information on the thermal biology of fish provides insights into their distribution, habitat use and bioenergetics, which ultimately drives growth, foraging, predator escape and reproductive investment. Temperature is dynamic, changing on a diel and seasonal basis. Moreover, for the next two decades a warming of approximately 0.2°C per decade is projected for a range of greenhouse gas (GHG) emission scenarios in relation to climate change (IPCC 2007). Some regions are likely to be especially vulnerable to climate change because of sensitivity, compounding stressors, or geographic exposure.

1.2 Tropical Ecosystems

Tropical and sub-tropical regions, such as the Caribbean, have characteristics that make them uniquely vulnerable to the anticipated effects of climate change (IPCC 2007). 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. These ecosystems 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). In the specific case of 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). How will changing temperatures affect the spatial and temporal distribution as well as the energetics of tropical fish species located in particularly vulnerable environments?

1.3 Trade-offs Between Generalists and Specialists

Animals often concentrate their fitness enhancing activities, such as growth, mating, foraging, and reproduction, over a narrow and preferred range of temperatures (Gilchrist 1995). There are, however, different temperature preference strategies with both costs and benefits. Some individuals specialize in a narrow range of environmental temperatures, concentrating their fitness enhancing activities in limited periods of favourable conditions (Gilchrist 1995). Species may also evolve as generalists and be active over a broad range of conditions (Gilchrist 1995). While constant environments favour specialists, temporal variation usually selects for generalists. The trade-offs between generalists and specialists originate from the structure and function of enzymes: an enzyme with higher conformational stability functions better at high temperatures, while an enzyme with lower conformational stability functions better at low temperatures (Angilletta et al. 2003). Orthologous allozymes are produced when a mutation alters an enzymes structure; these allozymes can enhance performance at some temperatures but reduce performance at others (thermal specialization) (Angilletta et al. 2003). Gene replication can lead to paralogous isozymes, which enable an organism to operate over a wider range of temperatures (thermal generalization) (Angilletta et al. 2003). Despite the advantages of isozymes, they require additional resources for synthesis, otherwise an organism will not be able to increase performance in one range of temperatures without decreasing its performance in another (Angilletta et al. 2003). A specialist-generalist trade-off is characterized by the fact that neither genotype outperforms the other at all temperatures (Angilletta et al. 2003).

Thermal tolerance windows of species differ depending on their range of natural environmental temperatures and tolerance windows are wider in tropical and temperate eurythermic species compared to polar stenotherms (Portner et al. 2006). Life in cold water is a severe challenge to organisms and forces them to specialise to living in such low temperatures (Portner et al. 2006). Eurytherms tolerate wider temperature fluctuations, and temperate species are able to dynamically shift their tolerance window between summer and winter temperature regimes (Portner 2002). The reasons for thermal specialisation based on geographical distribution still need to be identified, but limited oxygen availability and aerobic scope are crucial in limiting thermal tolerance (Portner 2002).

1.4 Thermal Tolerance - Adaptation and Acclimatization

Temperature is one of the most important abiotic factors for fish because they are ectothermic and the body temperatures of ectotherms conform to environmental temperatures (Kieffer 2000). Extreme temperatures impose limitations on organisms at high temperatures through irreversible protein denaturation and death as well as at low temperatures through the inactivation of proteins

(Have 2002). Fish often experience large temperature changes within their life history, either acutely or seasonally, and survival is possible through adaptation and acclimatization (Kieffer 2000). Acclimatization can be thought of as the compensatory response to prolonged temperature changes and requires phenotypic adaptations, or rearrangements of form and function, to improve function in the new thermal habitat (Portner et al. 2006).

Within an organism the crucial mechanisms of temperature adaptation should be visible in all tissues supporting the functional coordination of the fish (Portner 2002). Beyond a fish's thermal window or critical temperature, passive tolerance can only ensure temporary individual survival (Portner et al. 2006). Oxygen availability most likely sets the limits of extreme temperature intolerance and defines temperature adaptation and limitation (Portner 2002). It has been suggested that thermal sensitivity becomes evident at the highest functional level possible; ventilation and circulation (Portner 2002). Portner (2002) hypothesized that shifts in thermal tolerance windows is mostly caused by changes in tissue mitochondrial densities and functional properties, which has consequences for cell and tissue function as well as central functions like nervous control, circulation, and respiration. Changes in mitochondrial functions not only explains shifts in thermal tolerance limits but also contributes to tradeoffs in energy budgets with consequences for growth, fecundity and other vital ecological functions (Portner 2002). The onset of hypoxia and mitochondrial anaerobic metabolism indicates a transition to passive and temporary extreme temperature tolerance and indicates a mismatch in oxygen supply and demand (Portner 2002). An exponential increase in oxygen demand is reflected in aerobic scope loss, reduced spontaneous activity like feeding, reduced cardiac capacity and finally a collapse of physiological functions (Portner 2002). In combination with mitochondrial changes, cells also exhibit thermal compensation for maintaining homeostasis through modifications in lipid saturation, kinetic properties of metabolic enzymes, contractile proteins, and transmembrane transporters (Portner et al. 2006). These processes define the limits of thermal tolerance and contribute to functional optimization (Portner 2002).

Despite being eurytherms, increasing evidence suggests that species located in tropical regions might be sensitive to just a couple degree temperature increases, due to their evolution in thermally stable environments (Donelson et al. 2011; Sunday et al. 2011). Some tropical species 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 variation, 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 or acclimatization temperature. Each species will exhibit different capacities for acclimatization based on how close they are currently living to their thermal tolerance limits. Undoubtedly, at high temperatures that approach the critical thermal maxima of fish, they will be excluded from certain habitats and experience changes in energy allocation (Portner and Farrell 2008). While there exists a generic understanding of the potential impacts of temperature and climate change, understanding how temperature will affect fish with different life-histories and residing in different regions is still needed.

1.5 Swimming Energetics – Critical Swimming Speed and Scope for Activity

Environmental water temperature is a critical determinant of the distribution and abundances of biota through a profound effect on their physiology (Farrell et al. 2008). Quantifying this relationship between animal fitness and temperature has proved to be challenging. Important 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 (Donelson et al. 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 (Farrell et al. 2008). The operational definition of routine metabolic rate for this study was a metabolic rate that incorporates neither locomotion nor digestion, but is measured during the day. 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 swimming speed decrease at temperatures above and below the optimal temperature for that particular species. Insufficient scope for activity leads to the use of anaerobic metabolism, exhaustion and even death (Farrell et al. 2008). Therefore, whole-animal tolerance and survival to temperature extremes is restricted as energy allocation is limited (Farrell et al. 2008).

Swimming speed can be enhanced through several anatomical and physiological modifications. Factors such as, muscle length and area, tendon thickness, angles and composition of muscle fibers, and changes in the neuromuscular junction all influence locomotion and can be enhanced by allocating a greater amount of energy to skeleto-muscular tissue (Angilletta et al. 2003). In combination with the role muscles play in swimming speed, body size and shape, diet or nutrition, water quality and finally temperature have all been shown to limit both the exercise performance and recovery of exhaustive exercise (Kieffer 2000). Swimming activity in fish is normally aerobic and supported by red musculature, however burst type exercise can exceed a fishes aerobic capacity and lead to anaerobic glycolysis within the white muscle (Kieffer 2000). Since white muscle energy stores are used to support anaerobic swimming, energy reserves of glycogen, ATP, and PCr are critically limiting, along with the accumulation of metabolic end-products (Kieffer 2000). Unlike aerobic type swimming, anaerobic exercise can only be maintained for short periods and results in fatigue (Kieffer 2000). Because exercise involves the interactions of many body systems, it is considered an integrated measure of an animal's fitness in a specific environment (Kieffer 2000). Temperature not only influences the storage, utilization and recovery of white muscle fuels (glycogen, ATP, PCr) but it also influences the removal of metabolic end-products, therefore undoubtedly limiting a fish's ability to perform anaerobic exercise (Kieffer 2000).

For fishes, it is well established that extreme temperatures limit energy allocation, thus affecting fitness (Portner 2002). The energetic costs of homeostatic maintenance are the major determinants of the quantity of energy available for other functions and activities (Portner et al. 2006). Fitness can be defined as lifetime reproductive success, which from an energetics perspective translates to optimal resource and energy allocation towards growth and reproduction (Kozlowski 1996). In this context, fitness in a fluctuating environment depends on both tolerance (survival probability as a function of temperature) and performance (the capacity to reproduce at various temperatures) (Gilchrist 1995). When fish are exposed to temperature changes, they can attempt to achieve optimal performance and homeostasis by altering either their behaviour (preference/avoidance) or their physiology (adaptation and acclimation) (Lee et al. 2003). While these alterations have the potential to produce benefits to the individual in terms of handling temperature change, there are also associated costs. There are possible energetic costs associated with modifications for which the energy used could have been spent on other functions. Reductions in scope for activity and swimming performance have consequences for processes such as immuno competency, foraging, reproduction, growth and predator escape (Donelson et al. 2011).

1.6 Bonefish *(Albula vulpes)*

An example of a tropical species that is both economically and ecologically significant but for which information on thermal habitat requirements is lacking, is the bonefish *(Albula vulpes)*. Bonefish are a species that inhabit tropical and subtropical coastal marine environments from nearshore shallows to offshore waters (Humston et al. 2005). Bonefish utilize mangrove creeks as these habitats provide an abundance of prey and protection from large predators. Bonefish move in and out of mangrove creeks with the incoming and outgoing tides to feed (Danylchuk et al. 2004). 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 (Murchie et al. 2009). 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 (Danylchuk et al. 2011). Despite their recognized importance, there is limited information on their spatial dynamics and distribution, as well as energetics, especially when compared to other species targeted by recreational anglers (Murchie et al. 2011).

1.7 Thermal Profile of Wild Bonefish

Previous work has revealed that at high temperatures that approach the critical thermal maxima of bonefish, they tend to be excluded from creek habitats. Murchie et al. (2011) studied the thermal biology of bonefish using laboratory work and field studies with acoustic telemetry. The critical thermal maximum (CT_{max}) for bonefish was 36.4±0.5°C and 37.9±0.5°C for fish acclimated to 27.3±1.3°C and 30.2±1.4°C, respectively. Those tolerances were below maximal temperatures recorded in the tropical tidal habitats where bonefish frequently reside (i.e., up to 40.6ºC) (Murchie et al. 2011). This research also revealed that physiological responses to standardized capture stressors were more severe at higher water temperatures and that post-release tagging mortality also increased with water temperature (Murchie et al. 2011). Collectively, these data illustrate some of the ways in which bonefish spatial ecology and responses to stressors are mediated by water temperature. This study by Murchie et al. (2011) 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 have provided the opportunity to reconstruct the thermal history of bonefish over periods that cover an entire year.

1.8 Research Objectives

The goal of this research was to generate knowledge on the environmental physiology of bonefish with a specific focus on thermal biology. This was accomplished with a laboratory study, using a swim tunnel, with the purpose of characterizing bonefish swimming energetics with respect to temperature and to identify thermal optimum as well as their critical temperature. It was hypothesized that as temperatures exceed their thermal optimum, both critical swimming speed and scope for activity will decrease. A field study was also performed, using iButtons, with the purpose of describing the annual thermal experience of wild bonefish. The data were then compared to temperatures from within the tidal creek habitats to examine habitat use, distribution, and the potential effects of climate change. Combined, these studies can determine if the mean temperature bonefish experience on a seasonal basis corresponds to their thermal optima. Given the ecological and economic importance of bonefish, a lack of information on their thermal tolerances demanded an investigation into their thermal biology and spatial ecology over larger time frames. Collectively this information will augment the understanding of bonefish thermal biology and guide conservation strategies in response to climate change.

2.0 METHODOLOGY

2.1 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 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. 2007). Bonefish, *Albula vulpes*, were captured from local tidal mangrove creeks on an outgoing tide using a large seine net (13mm mesh, 46m long; 32mm mesh, 76m long; 70mm mesh, 61m long) (Murchie et al. 2009). These tidal creeks are characterized by sandy beach, turtle grass *(Thalassia testudium)* and surrounded primarily by red mangroves *(Rhizophora mangle)* (Danylchuk et al. 2007). Following capture bonefish were transferred into a flow-through holding pen (1.3x0.8x1.25m tall, 31mm extruded plastic mesh) to provide them with ample oxygen and facilitate handling of the fish. 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).

2.2 Swim Tunnel – Fish Transportation and Holding

Bonefish (average 405mm fork length; range = 336-507mm) were then transferred into coolers on a boat for transportation back to the CEI seawater facility. Water changes were performed periodically (approximately every 5 minutes) 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, with mean water conditions of pH 8.3, 6.2mg/l dissolved oxygen, 36.7ppt salinity, and 0.25ppm ammonia, at ambient water temperatures. Fish were given a minimum of 24 hours to acclimate to laboratory conditions before experimentation.

2.3 Swim Tunnel

Fish were swum in a 108.74 litre modified Blazka-type swim tunnel, similar to that described by Booth et al. (1997). The transparent swim chamber had a 31.9cm internal diameter and was 136cm in length, with a plastic grid at each end. Water speed was uniform across the swim tunnel throughout the speed range used in these experiments. The 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, 0-120Hz) whose readings (Hz) were calibrated with known water velocities, as measured with a mechanical water flowmeter (General Oceanics, Miami, FL).

2.4 Swimming Protocol

Individually, fish were moved to the swim tunnel where they recovered overnight (~12h) at a water speed of 1cm/s (Lee et al. 2003). The following day, each bonefish performed a modified ramp-U_{crit} test to assess their critical swimming speed (Jain et al. 1997). The ramp-U_{crit} protocol involves increasing water speed in 15cm/s increments every 15mins until exhaustion (Lee et al. 2003; MacNutt et al. 2006). Exhaustion was deemed to have occurred when the fish's tail touched the back grate for more than 20 seconds of contact.

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

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

where ui is the water velocity of the last fully completed increment (cm/s); uii is the water velocity increment (15cm/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 (15min). U_{crit} was corrected for the solid blocking effect according to the calculations by Bell and Terhune (1970):

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

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.

2.5 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 1mg/l accuracy. Two MO_2 measurements were taken during each experiment; 1) routine MO_2 and 2) maximum MO_2. Measuring oxygen consumption immediately prior to experimentation provided routine MO_2 measurements. Oxygen consumption measured at U_{crit} was designated as the maximum MO_2 measurement. The first 10 minutes 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 swim tunnel was thoroughly rinsed between experiments 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:

$$MO_2 = \Delta[O_2]v/mt,$$

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 1kg=1l), m is the fish's weight (kg), and t is time (min). Scope for activity was then calculated as the difference between MO_{2max} and $MO_{2routine}$ (Lee et al. 2003).

Following swim tests, fish were removed from the swim tunnel, weighed (kg), and measured for fork length (FL; cm), total length (TL; cm), width (w; cm) and maximum depth (d; cm) before release. Individual fish were only run once through the swim tunnel due to survival concerns.

2.6 Swim Tunnel Temperature Manipulation

Experiments were performed between October 16, 2012 and November 5, 2013 at ambient water temperatures (20.7-30.3°C). Swim tunnel experiments were performed at ambient water temperatures throughout the year in order to assess differences in bonefish swimming speed in different seasons. Additional experiments were performed during the summer at adjusted higher temperatures. Heaters were used to gradually increase water temperatures overnight to a maximum of ~6°C above ambient to extend the temperature range (Lee et al. 2003). Adjusted treatment temperatures ranged between 30°C and 36°C considering bonefish maximum critical temperatures are ~38°C (Murchie et al. 2011).

2.7 Laboratory Data Analysis

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). The optimal temperatures (T_{opt}) were defined as the temperature corresponding to the peak 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. Bonefish metabolism was analyzed using a linear mixed effects model with swimming speed (cm/sec), temperature (°C), bonefish length (FL, 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. All statistics were performed using SigmaPlot 11.0 (www.systat.com) and R (www.r-project.org).

2.8 iButton Implantation

Bonefish (average 389±3mm fork length; mean±SE; range = 308-480mm), 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 iButton thermal loggers (iButton DS1921H, factory stated resolution=±0.1°C, accuracy=±1°C, Maxim Integrated Products, Inc., San Jose California, USA) to record temperature every 255 minutes for 362 days. IButtons were waterproofed using Plasti Dip (Performix Brand, Blaine MN) and had a diameter of 16mm, a height of 5mm and weigh ~1gram. Prior to surgery, individual bonefish were removed from the holding pen, anesthetized with MS-222 (concentrations where equilibrium loss occurred under 2 minutes) in a cooler (100 liters), and then placed on a surgery table. While on the surgery table, the fish's gills were supplied with fresh seawater using a recirculating pump. Surgeons wore vinyl gloves, and iButtons, along with surgical tools, were cleaned with iodine prior to every surgery to keep surgeries as clean as possible. To implant iButtons, a 1-2cm midline ventral incision was made posterior to the pectoral girdle (Wagner et al. 2011). Each incision was closed with 2 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 minutes per fish and were always conducted by the same surgeon. Post surgery, fish were transferred to a recovery flow-through holding pen (1.3x0.8x1.25m tall, 31mm extruded plastic mesh) for a minimum of 1 hour. Following the recovery period, all bonefish were released together to encourage schooling and protection from predators. After being at liberty with an implanted iButton, 8 bonefish were recaptured between July 16, 2012 and April 9, 2013. Fish were lethally sampled in order to retrieve iButtons, sex and measure the fish. IButtons were downloaded for analysis. IButtons were also strategically placed at various intervals within the mangrove creeks, at the water substrate interface, since bonefish are entirely benthic invertebrates. These iButtons were placed in the mangrove creeks where the bonefish were caught as well as neighboring mangrove creeks to obtain environmental comparison temperatures.

2.9 iButton Data Analysis

All data emanating from recovered iButton thermal loggers was imported into a database. Data were analyzed to yield information on seasonal variation in thermal conditions for each individual fish. Using a generalised additive mixed model (GAMM) the significant factors predicting temperature were identified. The significance of ten terms was tested, including: hour of the day, centered fork length, sex, tide, season, fish ID, centered fork length x sex, tide x hour, tide x day, and season x hour. Following backwards model selection, the least significant term was dropped, making the final model for thermal experience: Temp = f(seq2) + hour:season + hour + fishID. A dependency structure was added to the model to account for serial correlation between observations within the same animal. 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 created to estimate at which point bonefish began to expel their iButtons. Data obtained from bonefish were also compared to temperatures from the tidal creeks to assess current and future climate change affected thermal habitats.

3.0 RESULTS

3.1 Swim Tunnel

Regression analyses were performed, revealing a significant ($P<0.05$) bell-shaped relationship between U_{crit} and temperature (Fig. 1b) and a weakened relationship between scope for activity and temperature (Fig. 1d). The optimal temperatures (T_{opt}) were defined as the temperature corresponding to the peak of the regressions between U_{crit}, scope for activity and temperature.

Critical swimming speed was optimal (T_{opt}) at 28°C while scope for activity was optimal at 26.7°C (Fig. 1). The upper critical temperature for both U_{crit} and scope for activity was 36°C (Fig. 1). Critical swimming speed at T_{opt} was 96cm/s or 2.4BL/s while scope for activity at T_{opt} was 7.5mgO_2/min/kg (Fig. 1). Metabolic rates for routine ($MO_{2routine}$) and maximum (MO_{2max}) showed their greatest difference at approximately the T_{opt} for scope for activity and that difference narrowed as temperatures decreased and increased (Fig. 1c).

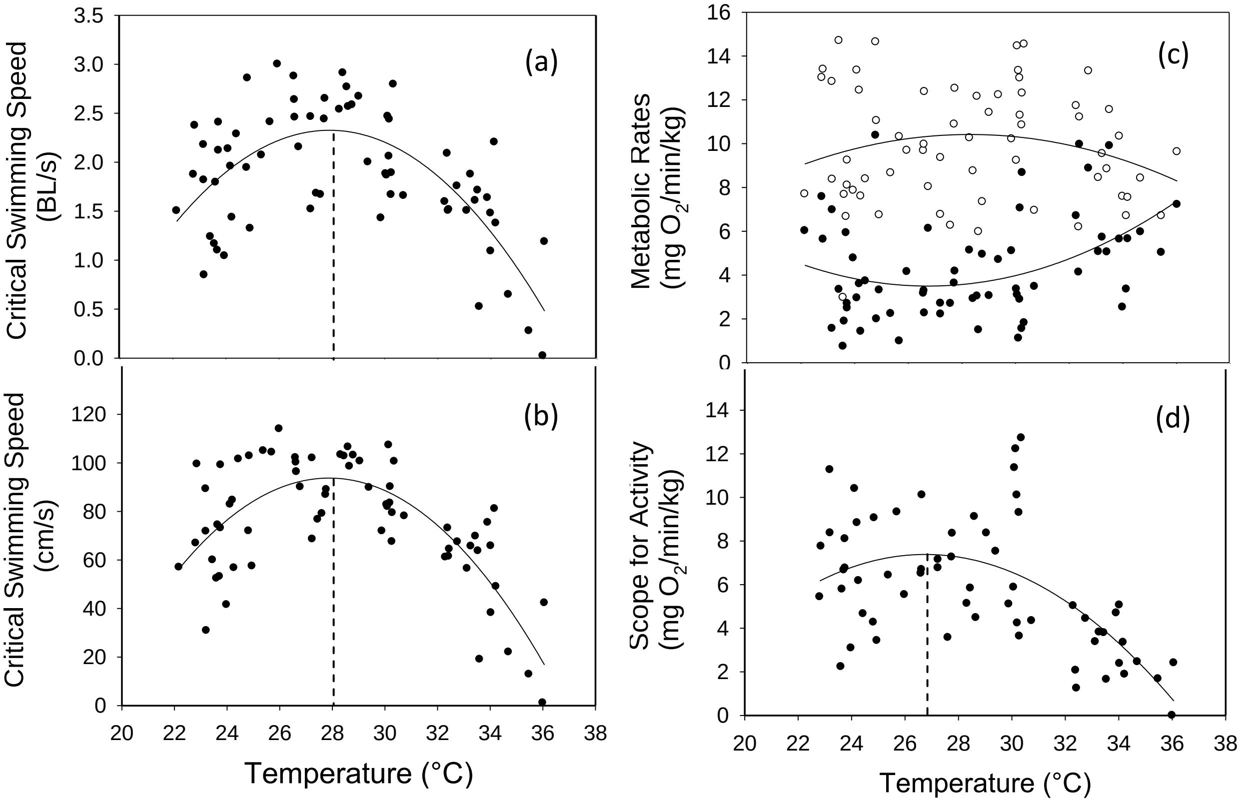

Figure 1. (a) Critical swimming speed in BL/s in relation to water temperature for bonefish. (b) Critical swimming speed in cm/s in relation to water temperature. (c) Routine (●) and maximum (○) oxygen consumption (MO_2) in relation to water temperature. (d) Scope for activity, the difference between 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)($y = -19.5 + 1.6x + -0.03x^2; r^2 = 0.47, P < 0.001$), (b) critical swimming speed (cm/s) ($y = -799.4 + 64x + -1.2x^2;\ r^2 = 0.56, P < 0.0001$), (c) routine metabolic rate ($y = 35.7 + -2.4x + 0.04x^2;\ r^2 = 0.16, P = 0.006$), maximum metabolic rate ($y = -18.1 + 2.0x + -0.04x^2;\ r^2 = 0.04, P = 0.33$) and (d) scope for activity ($y = -48.3 + 4.2x + -0.08x^2;\ r^2 = 0.35, P < 0.0001$).

MO_2 increased linearly with increasing swimming speed (Fig. 2). The effect of 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). As seen in Fig. 2, the higher temperatures of 36°C and the smaller fish exhibited higher metabolisms than lower temperatures and larger fish.

Table 1. Significant predictors of metabolism. Fixed effects: O_2 ~ Speed + FL + Temperature

	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

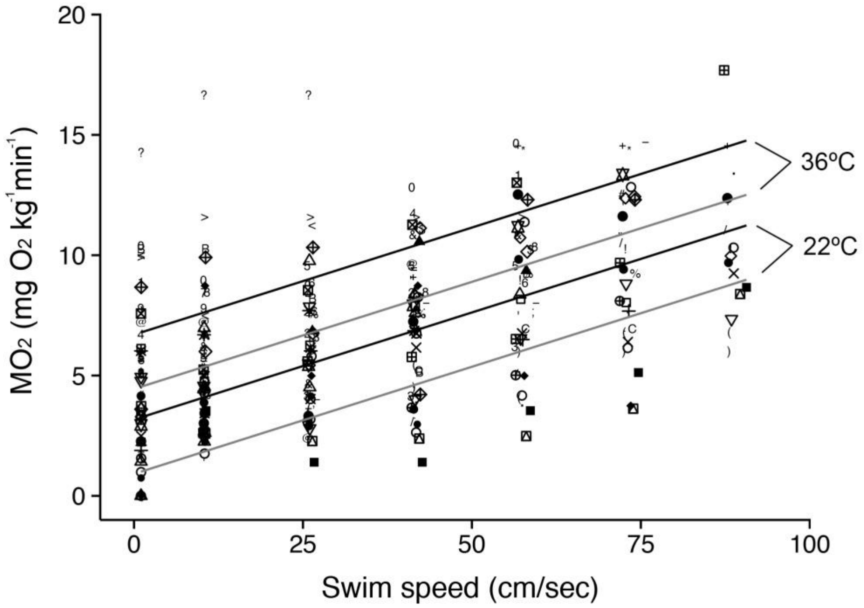

Figure 2. Rate of bonefish oxygen consumption (MO_2) across a range of swimming speeds, as well as temperature and fork length as significant predictors of metabolism. Grey lines represent the upper size range (50cm) and black lines the lower size range (34cm) of bonefish fork length.

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). The relationship between swimming speed and net cost of transport (COT_{net}) showed a typical 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 ($0.08mgO_2$/min/kg) for bonefish was a swimming speed of 70cm/s (Fig 3.). However, it is important to note that this quadratic relationship is largely driven by a couple data points at the lower swimming speeds.

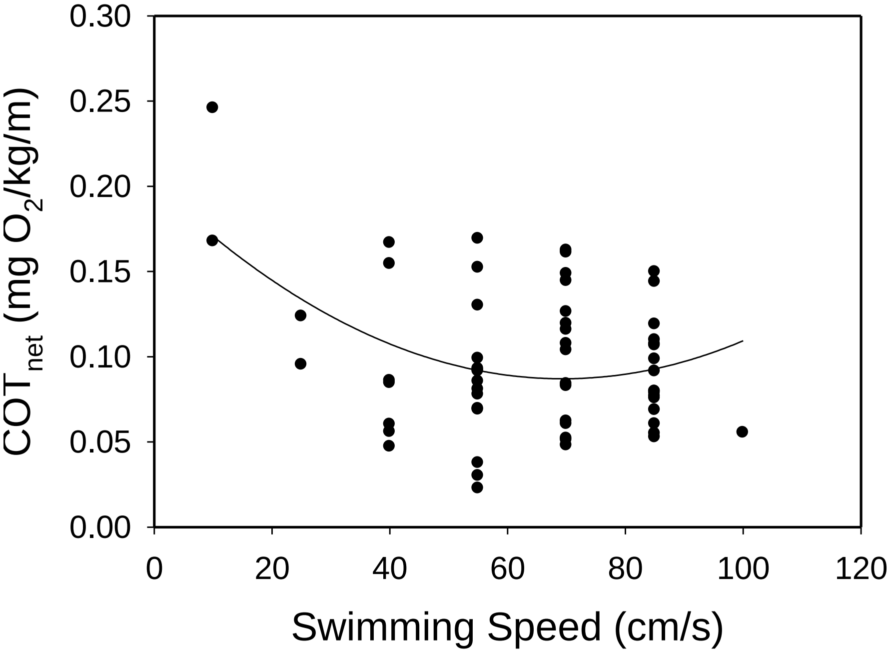

Figure 3. Relationship between net cost of transport (COT_{net}) and swimming speed for bonefish. A polynomial quadratic equation was fitted to COT_{net} ($y = 0.2 + -0.003x + 2.37E - 005x^2$; $r^2 = 0.16, P = 0.0079$).

3.2 Field Data

Of the 138 bonefish implanted with iButtons, 8 were recaptured with useable data, of which half were male and half were female, although no difference between sex was found (possibly due to a low sample size) (Table 2). None of the bonefish exceeded temperatures of 36°C which corresponds to their CT_{max} determined with the swim tunnel (Fig. 4). On a seasonal basis, the temperatures experienced by the bonefish, were on average for the spring 27°C (min=22.7°C, max=33.5°C), for the summer 30°C (min=24.4°C, max=35.7°C), for the fall 25°C (min=18.8°C, max=32.8°C) and for the winter 23°C (min=16.1°C, max=29.7°C) (Fig. 4). A clear and drastic decline in temperatures can also be seen between September and November, corresponding to Hurricane Sandy, which passed through The Bahamas on October 22, 2012 and dissipated on October 31, 2012 (Fig. 4).

Table 2. Summary of tagging and biological data for the 8 recaptured iButton fish used in this study. 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.

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

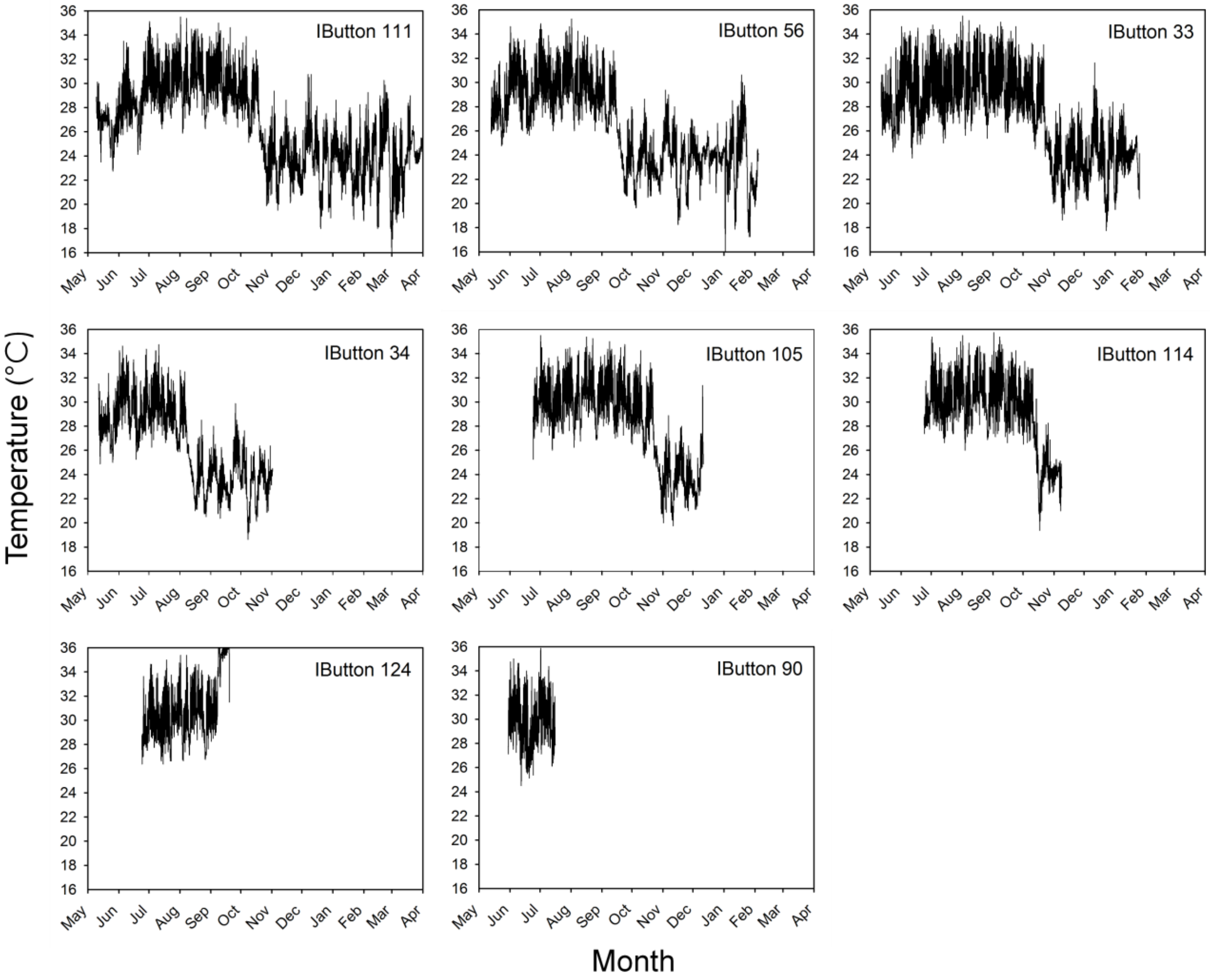

Figure 4. Thermal profiles of the 8 recaptured bonefish with iButtons. The dates represented are between May 11, 2012 and March 11, 2013.

The relationship between the temperatures experienced by bonefish throughout the year in relation to their critical swimming speed optimal temperature was determined using a generalized additive mixed model (GAMM) (Fig. 5). The models created for critical swimming speed and scope for activity were virtually identical; the critical swimming speed optimal temperature was arbitrarily chosen to represent the relationship. The model with a dependency structure was a significant improvement over the model without (df=1, *L*-ratio=5663.5, P<0.0001) (Table 3). As seen in Fig. 5, there are months where fish are consistently above their U_{crit} optimal temperature (i.e., throughout July and August in the summer) and other months where fish are consistently below (ie., throughout January in the winter).

Table 3. The importance of individual fixed terms for the mixed 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

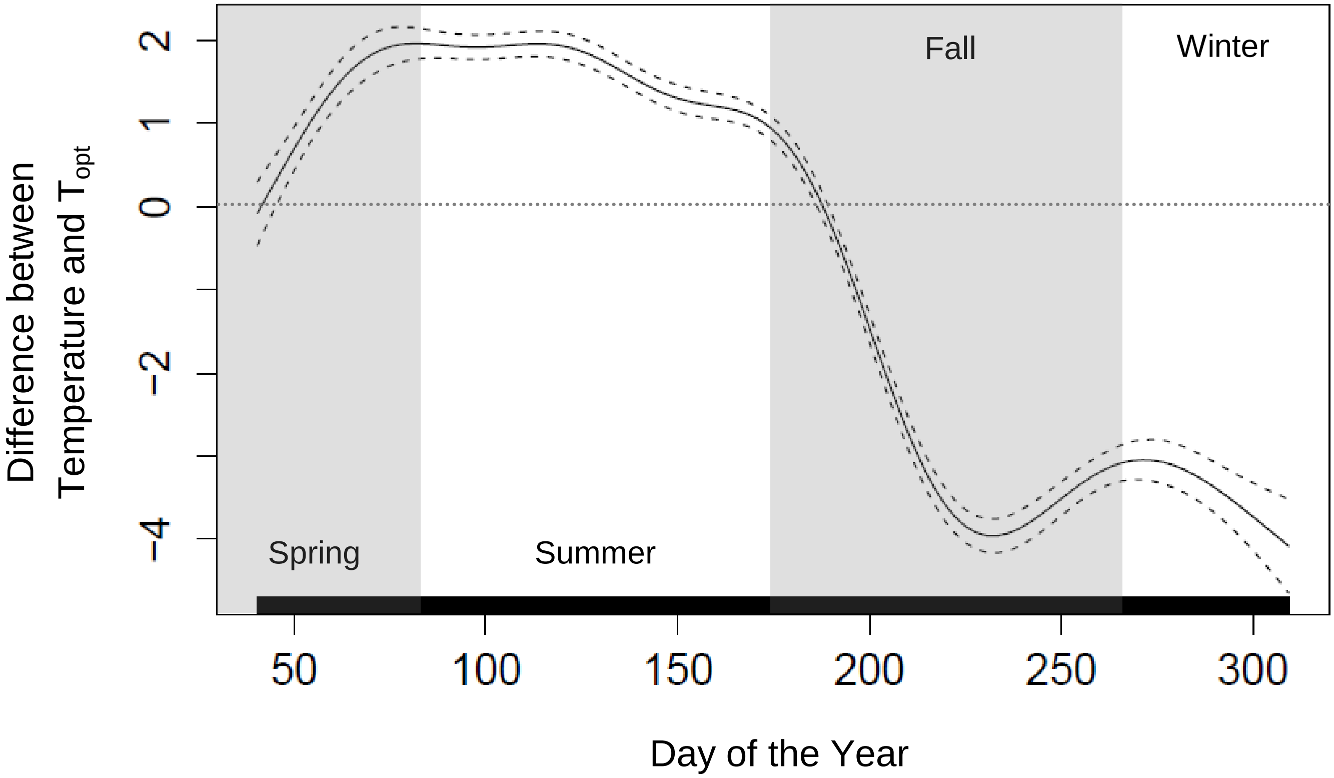

Figure 5. Estimated smoothing curves generated for bonefish thermal experience. Solid dark lines are the fitted values while dashed lines represent the approximate 95% point-wise confidence limits. Approximate significance of the smoothing term was $F_{8.79}=110.4$, $P<0.0001$. Model degrees of freedom 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. Seasons are delineated on the figure and the horizontal dotted line represents the optimal temperature for critical swimming speed.

Despite the utility of iButton implantation as a means for collecting thermal profiles of wild bonefish, there are a few previously unforeseen disadvantages. Of the 17 fish recaptured, 5 fish had expelled their iButtons and 4 iButtons recovered had errors and no data, leaving only 8 recaptured fish with iButtons that had useable data. After 220 days at liberty, more than 55% of the bonefish recaptured had expelled their iButtons, which was an interesting limitation of this study (Fig. 6).

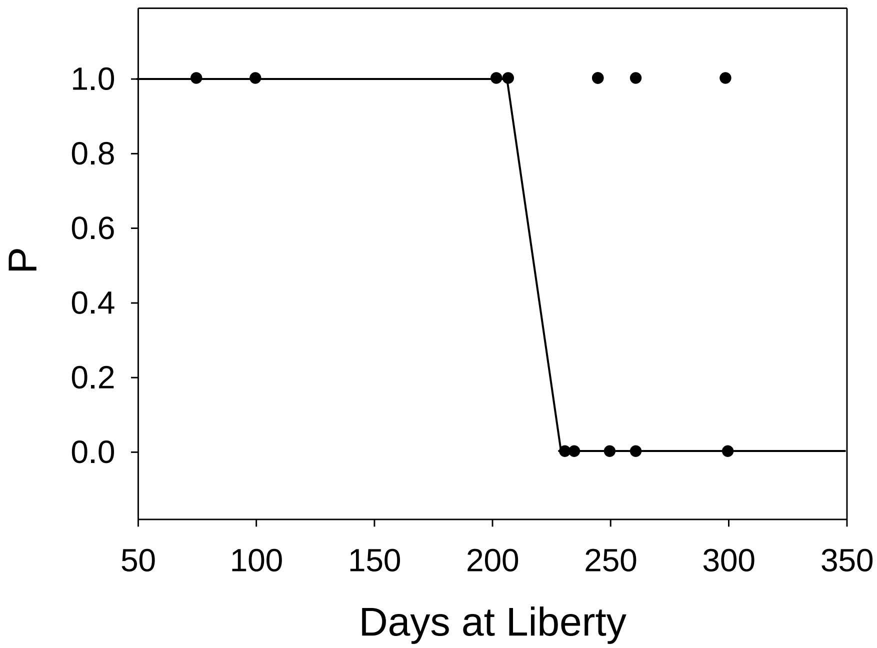

Figure 6. Logistic regression of iButton retention (represented by 1) and iButton expulsion (represented by 0) in bonefish at liberty.

4.0 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 using 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). While investigating the influence of temperature on metabolic rates, scope for activity and critical swimming speed; optimal and critical temperatures for bonefish were determined. Swimming speed and metabolic rates were also modelled to infer the effects of fish size and temperature on bonefish metabolism. This was accomplished with a laboratory study, using a Blazka-style swim tunnel. These laboratory data were then linked to the thermal experience of wild bonefish determined with surgically implanted iButton thermal loggers. A generalised additive mixed model (GAMM) was used to create a predictive model for the factors controlling temperature over different seasons in relation to bonefish optimal temperatures. Combined, these studies determined if the mean temperature bonefish experience corresponds to their thermal optima. The factors controlling optimal and critical temperatures, as well as fitness can also be inferred. These data 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. 2011).

4.1 Swimming Performance

Swimming performance and scope for activity are often used as a proxy for quantifying fish fitness in an ecologically relevant way (Donelson et al. 2011; Plaut 2001). Several studies report a temperature optimum for these specific physiological processes. 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 did indeed decrease. As seen in Fig. 1 for bonefish, 28°C was the optimum temperature for U_{crit} (N=69) and 26.7°C was the optimum temperature for scope for activity (N=49). The difference between the optimal temperatures for critical swimming speed and scope for activity challenges the oxygen and capacity limited thermal tolerance (OCLTT) hypothesis that scope for activity is an overarching physiological process that governs most other performances (i.e., including swimming performance, growth, digestion, reproduction, immune function, muscular activity, behaviour) (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 (Clark et al. 2013; Eliason et al. 2011). 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 is the case in this study.

For both U_{crit} and scope for activity, the maximum critical temperature (CT_{max}) for bonefish was 36°C (Fig. 1). This CT_{max} 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. 2011) and CT_{min} of 14.07°C and CT_{max} of 38.05°C (Shultz, unpub. data). However, both these studies used loss of equilibrium as their proxy for determining critical temperatures, instead of a physiological performance, such as swimming speed. In comparison to other species, bonefish thermal tolerances and critical temperatures are relatively conservative. Twenty-two 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. Nilson et al. (2009) found that 2 species of cardinal fish, *Ostorhinchus cyanosoma* and *Ostorhinchus doederleini*, had a maximum critical temperature of 33°C. For 15 species of reef fish, including wrasses, snappers, cardinalfish, gobies, mojarra and many others, maximum critical temperatures ranged between 34.7°C and 40.8°C (Mora and Ospina 2001).

Intuitively, at higher temperatures and with smaller fish, bonefish metabolism was higher, in comparison to lower temperatures and larger fish (Fig. 2). Metabolism as a function of body size and temperature is a well established relationship. Gillooly et al. (2001) recognized that metabolic rate, the rate at which organisms transform energy and materials, is predominantly determined by two interacting processes: the Boltzmann factor, which describes the temperature dependence of biochemical reactions, and the quarter-power allometric relationship, which describes how biological rate processes scale with body size.

The net cost of transport (COT_{net}) also changes at varying swimming speeds (Fig. 3), with the lowest COT_{net} for bonefish at a speed of 68cm/s or 1.8BL/s. COT_{net} provides an index of overall swimming efficiency, the lower the cost of transport value, the more efficient the locomotion (Claireaux et al. 2006). The COT_{net} for multiple stocks of sockeye and coho salmon ranged between 1.0 and 1.2BL/s, which is lower relative to bonefish, however salmon must make energetically costly upriver migrations for spawning and may have evolved as slightly more efficient swimmers (Lee et al. 2003).

4.2 Swimming Energetics

Critical swimming speed (U_{crit}) is a standard measurement to quantify the swimming capabilities of fishes (Plaut 2001). Swimming performance is considered a main character determining survival as it enables predator escape, foraging, finding a mate, and avoiding unfavorable conditions (Plaut 2001). During a U_{crit} test, the aerobic demands of swimming increase with swimming speed up to a maximum oxygen uptake, which is met using cardiorespiratory adjustments (Jain and Farrell 2003). Simultaneously, white muscle recruitment and anaerobic metabolism increasingly support the greater muscular power output near U_{crit}, ultimately ending in exhaustion (Jain and Farrell 2003). Along with these there are three physiological changes that occur in fish when exposed to changes in temperature: 1) changes in their mechanical power output from aerobic muscle, 2) limitations on the neural control of locomotory muscle and 3) limitations in the respiratory and circulatory systems in supplying oxygen (Jain and Farrell 2003). Although the interpretation of critical swimming speed results is limited since it does not take into account all the variables crucial for survival, U_{crit} results provide a relative index by which the physical status and fitness of the fish can be quantified and compared in an ecological context (Plaut 2001).

At the bonefish's optimal temperature, their U_{crit} was 96cm/s or 2.4BL/s and their highest recorded U_{crit} in this study was 114cm/s or 3.0BL/s (Fig. 1). In comparison to multiple stocks of sockeye and coho salmon whose U_{crit} ranged between 89.9 – 136.6cm/s or 1.4 – 2.3BL/s, bonefish critical swimming speeds are relatively impressive (Lee et al. 2003). While salmon must make upstream migrations for spawning, bonefish live in high predator areas with limited cover, resulting in high burst swimming speeds for predator escape.

4.3 Respiratory Energetics

Two key physiological parameters characterize the boundaries of a fish's capacity to uptake oxygen: routine metabolic rates and maximum metabolic rates. Routine metabolic rates correspond to the minimum maintenance metabolism of a fish during routine activities, whereas maximum metabolic rates correspond to a fish's maximum rate of oxygen consumption (Roche et al. 2013). Once routine and maximum metabolic rates are measured, they can be used to calculate a fish's scope for activity, which determines the range of metabolic energy available for aerobic activities (Roche et al. 2013). A decreased scope for activity is hypothesized to be the key physiological mechanism determining a fish's response to temperature change (Nilsson et al. 2009). At higher temperatures, beyond a fishes T_{opt}, a reduced scope for activity occurs because of the limited capacity of the circulatory and ventilator systems to keep up with the increased demands for oxygen, resulting in hypoxemia (Farrell et al. 2008; Nilsson et al. 2009). Not only does basal oxygen demand continue to increase, but cardiac pumping capacity plateaus and then collapses, leading to anaerobic metabolism, exhaustion and even death (Farrell et al. 2008). An animal's tolerance to extreme temperatures becomes limited as energy allocation to essential tissues also become limited (Farrell et al. 2008). This reduced the energy devoted to survival processes, such as growth and reproduction, having potential consequences for population sustainability (Nilsson et al. 2009).

Both critical swimming speed and scope for activity have optimal temperatures where their physiological performance is maximized, thus optimizing fitness (Clark et al. 2013). Energetic efficiency, scope for activity and swimming performance therefore all play a role in natural selection (Murchie et al. 2011). For fishes, it is well established that extreme temperatures limit energy allocation, thus affecting fitness (Portner 2002). When fish are exposed to temperature changes, they can obtain optimal performance by altering their behaviour or physiology (Lee et al. 2003). These alterations have energetic costs and consequences for performance attributes. Therefore fish experiencing warmer water temperatures will have less energy available resulting in fitness level implications such as lowered competitiveness, immune competence, foraging, reproduction, growth and predator escape (Hasler et al. 2012). While both critical swimming speed and scope for activity are limited in that they cannot possibly take into consideration all the processes fundamental to animal survival, they are important proxies for quantifying fitness.

4.4 Thermal Biology of Bonefish in the Field

According to the iButton thermal profiles, on an annual basis, bonefish did not experience temperatures below 14.5°C or above 35.8°C (N=8) (Fig. 4). IButtons were also placed within the tidal creeks to get an idea of the temperature profiles in the bonefish's feeding habitats. 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. (2011). 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}. On a seasonal basis, the temperatures experienced by bonefish, were on average 27°C for the spring, 30°C for the summer, 25°C for the fall, and 23°C for the summer (Fig. 4). Bonefish experienced fluctuations of up to 14°C per season and up to 8°C per day. 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 lines up with the considerably lower temperatures experienced by bonefish throughout the winter months (Fig. 4). While bonefish spawning is definitely linked to the lunar cycle, it could also reflect a need for lower temperatures when their scope for activity is lower and foraging is abundant since they are never excluded from creeks at cooler temperatures. The bonefish thermal profiles also showcase a drastic and seemingly sudden decline in temperatures between September and November (Fig. 4). This temperature decline corresponds to Hurricane Sandy, which passed through The Bahamas between October 22 and October 31, 2012. It would be interesting to compare thermal profiles from years with and without hurricanes to see the effects on temperature and bonefish habitat use. Individual accumulated thermal units (ATUs) were also generated to assess differences between sexes of bonefish. The average ATU for male bonefish was 160.7, while the average ATU for female bonefish was 155.5 (Table 2). The negligible difference between ATUs infers no difference between temperatures experienced both sexes.

A GAMM predictive model was created to determine the factors controlling temperature over seasons in relation to bonefish thermal optima (Fig. 5). Similar to the ATU, no sex related differences in temperature patterns were observed, this may have been due to the small sample size, 4 males and 4 females, or bonefish from both sexes follow similar thermal patterns. 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 regularly move into mangrove creeks at high tide to feed and then escape to deeper water during low tide. However, tides were also an insignificant predictor of 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 are consistently above their optimal temperature, while during other seasons, bonefish are consistently below their optimal temperature (Fig. 5). This data illustrates how flexible fish are to our theoretical values of optimal temperatures. While it obviously is not expected that fish will remain directly at these optimal temperatures, it does suggest that many other factors contribute to fish optima and dictate behaviour other then temperature, such as light, foraging, and predator avoidance.

4.5 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 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, 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 (IPCC 2007). 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. Collectively, 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. 2011). 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. 2011). 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).

4.6 Future Research

With respect to future research it is worth examining the disadvantages of iButton implantation with bonefish. One limitation of this study is the relatively small sample size, with only 8 recaptured fish with usable iButtons and data. It is interesting that after 220 days at liberty; more than 55% of the bonefish recaptured had expelled their iButtons (Fig. 6). This can be remedied in the future by concentrating recapture efforts earlier then the 220 day bench mark. Another constraint with implanting iButtons is the potential for iButton malfunction. More importantly, this finding suggests that biotelemetry studies, which are common for bonefish, may be unlikely to be successful in the long-term. Indeed, few studies have been able to track bonefish across multiple years and they often conclude movement or mortality. These data suggest that expulsion of tags may occur which requires revisiting intracoelomic implantation as the primary means of tagging bonefish.

In the future it would also be of interest to determine whether population specific differences in bonefish exist. Stock specific differences in many species of salmon has been repeatedly found for populations migrating to different spawning grounds (Eliason et al. 2011; Farrell et al. 2008; Lee et al. 2003). Eleuthera, in The Bahamas, is an island exposed to drastically different ocean environments, depending on the coast. The east coast is exposed to the Atlantic Ocean, with proximity to deeper, cooler water, while the majority of the west coast is sheltered and exposed to a protected shallow sound. Assessing the thermal profiles and tolerances of bonefish populations from habitats on both sides of the island could yield interesting results with certain populations having evolved specialized thermal windows.

To further expand our understanding of thermal tolerances in an under studied ecosystem, such as coastal sub-tropical flats, creating thermal windows for many species could be beneficial. Among-species 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). This would also increase the understanding of how species diversity and food webs might differ with climate change.

This information on the swimming energetics of bonefish can be combined with activity levels of wild bonefish to create a complete bioenergetics model for *Albula vulpes*. 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 (Mesa et al. 2013). A bioenergetics model would allow for modelling bonefish habitat use, movement and activity patterns as well as expand the understanding of sub-tropical coastal fish thermal tolerance (Murchie et al. 2011; Tomlinson et al. 2014).

4.7 Conclusion

In summary, bonefish optimal temperatures for critical swimming speed and scope for activity were similar, 28°C and 26.7°C respectively, and their critical temperatures were the same. These laboratory collected data correlated well with field data which showed that bonefish did not experience temperatures beyond their critical thresholds and spent the majority of their time in temperatures close to their optimums. Swimming speed and scope for activity proved to be good physiological proxies for quantifying fish fitness. Climate change has the potential to induce entire population shifts in fitness in response to temperature change. This information 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). Being the first paper to focus this type of swim tunnel research on bonefish, important thermal information has been gained on a coastal flats species which lays the ground work for future research.

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APPENDIX A

Pictures of Methods: Bonefish Capture, Swim Tunnel, iButton Implantation

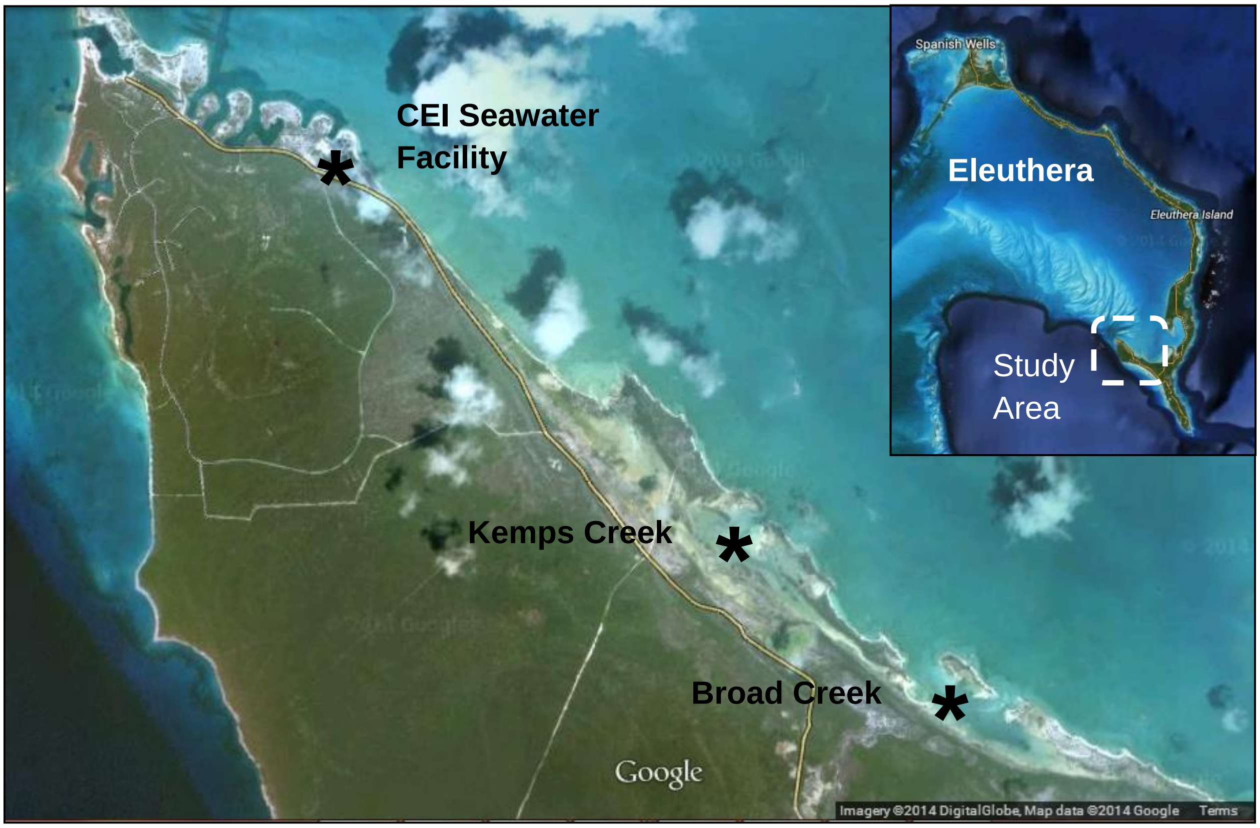

Figure 7. Map of the southern tip of Eleuthera, including Kemps and Broad creek where bonefish were captured as well as the CEI seawater facility where swim tunnel experiments were performed.

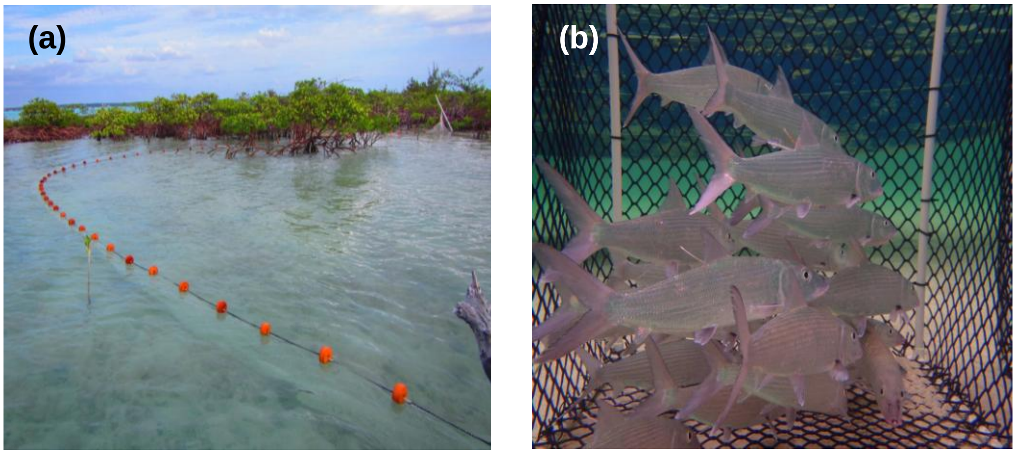

Figure 8. Bonefish capture. (a) A seine net placed across the mouth of a tidal mangrove creek. (b) Bonefish in a flow through holding pen.

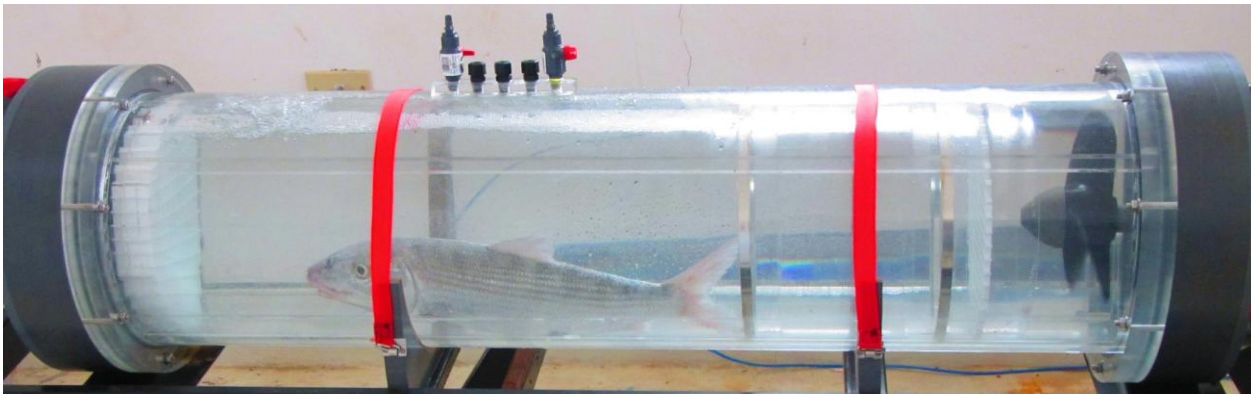

Figure 9. Bonefish in the swim tunnel.

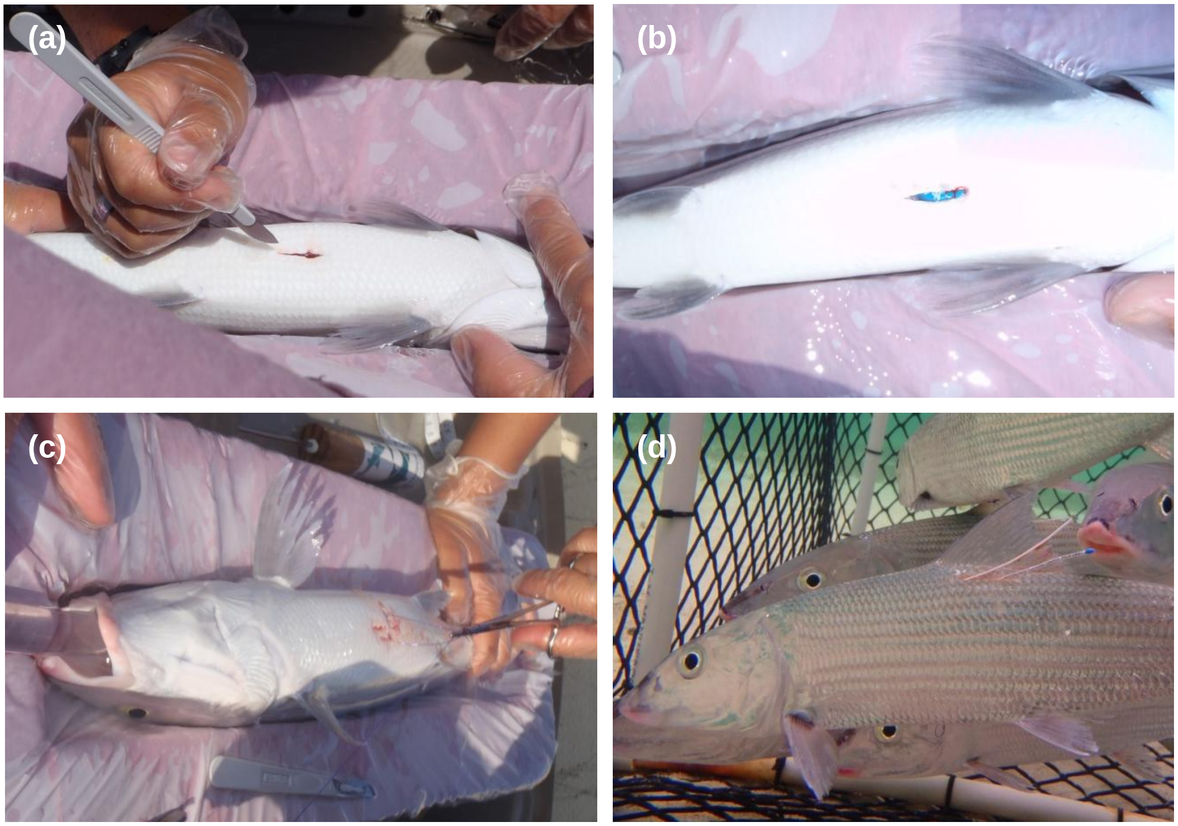

Figure 10. IButton implantation. (a) Incision made with scalpel for iButton. (b) IButton, covered in blue waterproofing plasti dip, implanted in bonefish. (c) Simple interrupted sutures closing the iButton incision. (d) Bonefish recovering in a flow through cage, externally tagged for identification.

APPENDIX B

Additional Publications Completed Throughout M.Sc. Program

Brownscombe, J. W., Bower, S. D., Bowden, W., Nowell, L., Midwood, J. D., Johnson, N., Cooke, S. J. *In Press.* Canadian recreational fisheries: 35 years of social, biological, and economic dynamics from a national survey. Fisheries 00:000-000.

Brownscombe, J. W., Nowell, L., Samson, E., Danylchuk, A. J., Cooke, S. J. *In Press*. Fishing-related stressors inhibit refuge-seeking behavior in released subadult Great Barracuda, *Sphyraena barracuda*. Transactions of the American Fisheries Society 00: 1-5.

Brownscombe, J. W., Samson, E., Nowell, L., Cooke, S. J. *In prep.* Conched out – activity and movement of queen conch in The Bahamas.

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