CrossMark

ORIGINAL PAPER

Thermal tolerance of nearshore fishes across seasons: implications for coastal fish communities in a changing climate

Aaron D. Shultz[1,2] · Zachary C. Zuckerman[2] · Cory D. Suski[1,2]

Abstract Global climate change is predicted to increase the variability in weather patterns with more extreme weather conditions occurring on a more frequent basis. Little information exists on thermal limits of fishes from highly variable environments. This study evaluated the thermal maximum and minimum of checkered puffers, yellowfin mojarra, schoolmaster snapper, and bonefish across seasons. Thermal scope (i.e., CT_{max}–CT_{min}) of nearshore fishes ranged from 24 to 28.6 °C across seasons, with thermal scopes typically being larger in the winter (January 1, 2012–March 22, 2012) than in the summer (June 26, 2012–November 9, 2012). Acclimatization response ratios (AZRR; $\Delta CT_{max}\ \Delta T^{-1}$ and $\Delta CT_{min}\ \Delta T^{-1}$) were typically greater than 0.60 for all species, a value greater than most previously reported for fish species from variable thermal environments. Present-day maximum and minimum temperatures in the nearshore environment are approximately equal to or exceed the thermal tolerance limits of the fish in this study, making thermal safety margins (TSM; i.e., the difference between thermal tolerance limit and extreme environmental temperature) very small or negative for nearshore fishes (TSM upper = −4.9 to 0.5; lower = −0.2 to 0.4). The IPCC's worse-case scenario will push maximum temperatures beyond the TSM of all nearshore fish in this study. Distribution of fishes in the nearshore environment in the future will depend on available thermal refuge, cost of migrating, and food web interactions. Overall, the thermal landscape in the nearshore environment in the future will likely benefit species with positive thermal safety margins that are capable of acclimatizing (e.g., schoolmaster snapper), while relatively intolerant species (e.g., bonefish) may inhabit these systems less frequently or will be absent in the future.

✉ Aaron D. Shultz
aaron.dean.shultz@gmail.com

1 Department of Natural Resources and Environmental Sciences, University of Illinois, 1102 S. Goodwin Ave., MC 047, Urbana, IL 61801, USA

2 Flats Ecology and Conservation Program, Cape Eleuthera Institute, Eleuthera, Bahamas

Introduction

Global climate change due to anthropogenic sources has altered weather patterns, the physical characteristics of the oceans, and the distribution of species (Roessig et al. 2005). In the next 100 years, marine temperatures are expected to increase by as much as 2 °C (IPCC 2013). Moreover, extreme weather events, such as major storms (i.e., tropical cyclones), floods, heat waves, and cold spells are expected to increase in both intensity and frequency as the climate changes (Knutson et al. 2010; Kerr 2011). Temperature is one of the main drivers behind the distribution of ectothermic species (e.g., fish) in the ocean (Somero 2010), and recent evidence indicates that climate change has altered the distribution and community interactions of some marine species (Perry et al. 2005; Poloczanska et al. 2013). For example, an extreme weather event increased seawater temperatures 3–5 °C above normal for more than 10 weeks along the West Coast of Australia, altering the distribution and abundance of demersal fish, sessile invertebrates, and seaweeds in habitats throughout this region (Wernberg et al. 2012). On the whole, environmental temperature may

exceed the physiological limits of species in the future, thereby affecting their biogeographical distributions.

The proximity of animals to their thermal limits, coupled with their potential to acclimatize to future environmental conditions, will both be factors influencing the reshaping of ecosystems as the climate changes (Stillman 2003; Somero 2012). Ectotherms in the tropics are expected to be adapted to a relatively narrow range of temperatures due to relatively small seasonal variation in temperature and, therefore, may not have the capacity to acclimatize to warming seas (Ghalambor et al. 2006). However, a recent meta-analysis indicates that the capacity to acclimatize to thermal environments in marine ectotherms is not dependent on latitude or thermal seasonality (Gunderson and Stillman 2015). Rather, tropical ectotherms from thermally stable environments are suspected to be vulnerable to climate change because they live closer to their thermal limits relative to organisms in temperate regions (i.e., smaller thermal safety margins; Pörtner and Farrell 2008; Nilsson et al. 2009; Pörtner and Peck 2010). However, recent evidence indicates that organisms from variable environments (e.g., intertidal zones) may be in closer proximity to their thermal limits relative to organisms from stable environments (e.g., coral reefs), making them vulnerable to temperature fluctuations associated with climate change (Madeira et al. 2012; Seebacher et al. 2014; Norin et al. 2014). Defining which species currently live near their upper thermal limit can provide a basis for evaluating how marine ecosystems will change in the future, especially during extreme weather events, and which species will be most vulnerable to local extinction (Somero 2010). Similarly, the ability of organisms to acclimatize (i.e., seasonal or long-term phenotypic alterations to new abiotic conditions) will play a role in buffering species against climate change (Hofmann et al. 2010). Previous research on fish acclimatized to the same temperature across different seasons has demonstrated differences in metabolic rates, indicating that seasonal shifts in physiological traits can occur (Evans 1984; Chipps et al. 2000). In addition, the upper thermal tolerance of several subtropical species of fish has been determined to be significantly higher during summer compared to winter, demonstrating a seasonal component to tolerance limits for these species (Fangue and Bennett 2003; Murchie et al. 2011). Species that have relatively high thermal maxima are expected to have a limited capacity to acclimatize to new conditions (Stillman 2003; Magozzi and Calosi 2014), but this assumption has not been tested on species found in variable thermal environments in nearshore subtropical ecosystems.

Nearshore ecosystems provide a number of important ecosystem services such as protecting coasts, sequestering carbon, and acting as nursery areas, yet they are some of the most anthropogenically disturbed ecosystems on the planet (Valiela et al. 2001; Barbier et al. 2011). Nearshore habitats are characterized by dynamic abiotic conditions, such as temperature, pH, and pCO_2, that fluctuate over diurnal, tidal, and seasonal scales (Lam et al. 2006). Though many species of nearshore fishes demonstrate an ability to cope with these dynamic conditions (Lam et al. 2006; Shultz et al. 2014), it is unknown if they have evolved similar physiological limits that will allow them to cope with extreme weather patterns predicted to occur in the future due to climate change. The duration and number of heat waves and cold snaps are expected to increase as the climate changes (Kerr 2011). For example, a record-breaking sea surface temperature anomaly in the Caribbean of 29.5 °C was recorded in September of 2010 (Trenberth and Fasullo 2012), and a 12-day cold snap in January of 2010, Florida, USA, decreased nearshore water temperatures by 11.2 °C in Butternut Key, Florida from 19.3 °C on January 1 to 8.1 °C on January 12 (NOAA 2010). Considering the proximity of fish to their thermal limits across seasons, coupled with understanding the physiological plasticity of fish to abiotic variables when acclimatized to seasonal conditions, will be important tools for evaluating the response of fish to the future oceanic conditions and extreme weather events associated with climate change (Pörtner 2002). Moreover, fish from highly variable environments, such as nearshore marine ecosystems and latitudes between 20 and 35 (i.e., subtropical regions), are underrepresented in the thermal tolerance literature (Sunday et al. 2011).

Based on this background, the objective of this study was twofold: (1) determine the critical thermal tolerance limits of four nearshore fishes across seasons, (2) relate these limits to current and projected thermal environments in the ocean. To do this, we defined the critical thermal maxima (CT_{max}) and minima (CT_{min}), and estimated thermal scope (CT_{max}–CT_{min}), acclimatization response ratios (AZRR), and thermal safety margins (TSM) of four common nearshore fishes across summer and winter seasons. Collectively, the outcomes of this research will help improve predictions of how species, fish communities, and ultimately ecosystems will respond to climate change.

Methods

This study was conducted at The Cape Eleuthera Institute (CEI) in Eleuthera, The Bahamas (N 24°50′05″ W 76°20′32″). All research conformed to the University of Illinois Institutional Animal Care and Use Committee protocol (Protocol # 09160). Fish [adult checkered puffer, *Sphoeroides testudineus* (Linnaeus, 1758) and adult bonefish, *Albula vulpes* (Linnaeus, 1758), and juvenile yellowfin mojarra, *Gerres cinereus* (Walbaum, 1792) and juvenile schoolmaster snapper, *Lutjanus apodus* (Walbaum, 1792)]

Table 1 Length (mean $\pm$ SE) of yellowfin mojarra, checkered puffer, schoolmaster snapper, and bonefish used in this study

Species	Season	Total length (mm)	Fork length (mm)	Range (mm)
Yellowfin mojarra	Summer	NA	133 $\pm$ 3	110–160
	Winter	NA	131 $\pm$ 5	85–168
Checkered puffer	Summer	173 $\pm$ 6	NA	107–202
	Winter	176 $\pm$ 3	NA	136–195
Schoolmaster snapper	Summer	147 $\pm$ 5	NA	115–190
	Winter	108 $\pm$ 3	NA	93–155
Bonefish	Summer	NA	389 $\pm$ 6	350–445
	Winter	NA	400 $\pm$ 5	355–469

Fish anatomy dictated the choice of metric used to measure each species: A fork length was generated for species that had a forked or furcate caudal fin, and a total length was taken for species with a truncate or rounded caudal fin. Each species in each season had a sample size of eight fish

Table 2 Final seasonal temperature (°C) prior to thermal tolerance assays of yellowfin mojarra, checkered puffer, schoolmaster snapper, and bonefish in the winter and summer

Season	Treatment	Acclimatization temperature (°C)			
		Yellowfin mojarra	Checkered puffer	Schoolmaster snapper	Bonefish
Winter	CT_{max}	24.2	23.8	24.6	23.8
	CT_{min}	23.6	22.5	23.4	23.7
Summer	CT_{max}	30	30.4	31	29.3
	CT_{min}	28.7	27.8	29.1	29.4

were collected from tidal creeks in the winter (January 1, 2012–March 22, 2012) and summer (June 26, 2012–November 9, 2012) by seining on an outgoing tide. These fish experience a range of temperatures in the nearshore environment in each season (winter: 21.2 $\pm$ 0.08 °C; mean $\pm$ SE, 11–35.7 °C; range, summer: 30.3 $\pm$ 0.06 °C; mean $\pm$ SE, 23.5–43 °C; range reported in Shultz et al. 2014). After capture, fish were transported to aerated holding tanks (3.7 m diameter × 1.25 m height, 13,180 L) supplied with fresh seawater (1800 L h⁻¹) drawn directly from the nearshore environment at CEI, and given 48 h to recover (Murchie et al. 2009). Fish held in the wetlab facility at CEI experienced typical day/night cycles in each season (Murchie et al. 2011), and fish were not fed during recovery or prior to experimentation. Seawater temperatures during recovery in the wetlab fluctuated daily (YSI 85, Yellow Springs Incorporated, Yellow Springs, OH) in both the winter (23.5 $\pm$ 1.1 °C; mean $\pm$ SD, 22.3–24.7 °C; range) and summer (29.5 $\pm$ 1.1 °C; mean $\pm$ SD, 26.4–32 °C; range).

Following recovery, eight fish of the same species and of similar size were placed into aerated, opaque, individual plastic chambers resting in a raceway (3.09 m length × 0.65 m width × 0.17 m height) continuously supplied with recirculating seawater (Eheim pump 1046A, 5 L min⁻¹) from a common reservoir (Igloo cooler 108 L), completing a closed water system (Vanlandeghem et al. 2010; Table 1). This system allowed for the critical tolerance limits of eight fish to be evaluated simultaneously,

and species were tested sequentially in each season. The temperature of seawater in the closed water system prior to experimentation was considered the acclimatization temperature for each species in each season (Table 2). Critical thermal tolerance limits were attained by gradually increasing/decreasing the temperature until a fish experienced a loss of equilibrium for 1 min (Murchie et al. 2011). Changes in seawater temperature (measured with a multiparameter meter, YSI 85, Yellow Springs Incorporated, Yellow Springs, OH) were achieved using either an immersion heater (Process Tech Heaters #H18T, 1800 W, 115 V, 15 A; Controller #NA30DX; Aquatic Ecosystems, Apopka, FL, USA) or heat exchanger in the common reservoir at a consistent rate of 0.18 $\pm$ 0.02 °C min⁻¹; mean $\pm$ SE (Beitinger et al. 2000; Murchie et al. 2011).

Statistical analyses

A t test was used to quantify differences in critical maxima/minima and thermal scope (i.e., CT_{max}–CT_{min}) for each species across seasons (Sokal and Rohlf 1995). Additionally, a t test was used to compare breadth in tolerance for each species across seasons (i.e., the absolute value of acclimatization temperature—critical thermal tolerance limit; Sokal and Rohlf 1995; Duarte et al. 2012), to determine which season fishes would be most at risk of exceeding their critical thermal limits. A small breadth in tolerance indicates that a species may be at risk to warmer or cooler temperatures in a season. Prior to running each t test, a Hartley F

Max test was used to verify equal variances across treatment groups (Hartley 1950), and a Shapiro–Wilk's test was used to determine normality of data (Sokal and Rohlf 1995). The magnitude of a species' ability to acclimatize to new thermal environments can be expressed as an acclimatization response ratio (AZRR; $\Delta CT_{max} \Delta T^{-1}$ and $\Delta CT_{min} \Delta T^{-1}$; Claussen 1977). These ratios were calculated across seasons to determine the relative acclimatization response of each species (Hopkin et al. 2006; Reyes et al. 2011), and a total AZRR score was calculated to evaluate the relative thermal plasticity of fishes within the nearshore ecosystem. Present-day thermal safety margins (TSM; summer CT_{max}—maximum environmental temperature and minimum environmental temperature—winter CT_{min}; Deutsch et al. 2008; Sunday et al. 2014) were calculated for each species using extreme temperatures in the nearshore environment that these fish inhabit (summer −43 °C; winter −11 °C reported in Shultz et al. 2014). Positive TSM values indicate that environmental temperatures do not exceed tolerance limits. Negative values indicate present-day

temperatures currently exceed tolerance limits, requiring fish to spend less time in this ecosystem and more time in thermal refugia (e.g., deeper/adjacent ecosystems; Sunday et al. 2014). All statistical analyses were performed using JMP 7.0.1 (SAS Institute Inc., 2005), all means are reported ± standard error (SE) where appropriate, and the level of significance for all tests (α) was 0.05.

Results

Yellowfin mojarra

The critical thermal maxima and minima of yellowfin mojarra differed significantly between seasons, and CT_{max} at which fish lost equilibrium was almost 5 °C greater in the summer than in winter (Fig. 1a; Table 3). Moreover, the upper breadth in tolerance (i.e., CT_{max}—acclimatization temperature) of yellowfin mojarra in summer (11 °C) was approximately 2 °C smaller than in winter (13 °C).
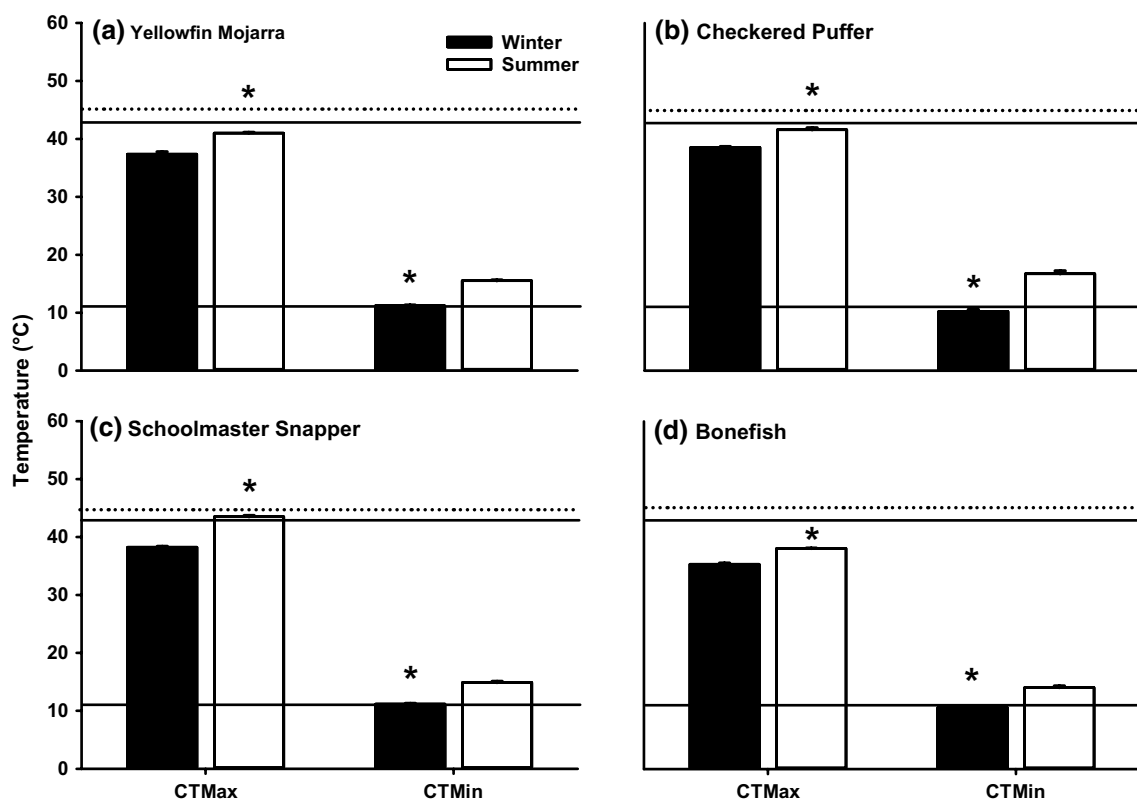

Fig. 1 Critical thermal limits of **a** yellowfin mojarra, **b** checkered puffer, **c** schoolmaster snapper, and **d** bonefish recovered in laboratory conditions in the winter (22.3–24.7 °C) and summer (26.4–32 °C). An *asterisk* denotes significant differences in CT_{max} and CT_{min} across seasons. Each treatment in each season had a sample size of eight fish. *Error bars* represent ±SE and are challenging to discern for CT data due to low variation across individuals. *Horizon-tal solid lines* indicate extreme minimum temperature in the winter and extreme maximum temperature in the summer in the nearshore ecosystem reported by Shultz et al. (2014). *Horizontal dotted line* signifies extreme maximum temperature in the summer plus the Intergovernmental Panel on Climate Change worst-case scenario for sea surface temperatures in 100 years

Table 3 Results of *t* tests comparing the seasonal variation in thermal scope (CT$_{max}$–CT$_{min}$), CT$_{max}$, upper breadth in tolerance (CT$_{max}$—acclimation temperature), CT$_{min}$, and lower breadth in tolerance (acclimation temperature—CT$_{min}$) of yellowfin mojarra, checkered puffer, schoolmaster snapper, and bonefish (summer vs winter)

Variable	Yellowfin mojarra		Checkered puffer		Schoolmaster snapper		Bonefish	
	T	P	T	P	T	P	T	P
Thermal scope	0.96	0.37	5.33	0.0002	6.33	<0.0001	2.43	0.0355
CT$_{max}$	8.68	<0.0001	9.20	<0.0001	22.28	<0.0001	12.86	<0.0001
Upper breadth in tolerance	5.19	0.0014	10.62	<0.0001	0.37	0.72	12.15	<0.0001
CT$_{min}$	15.29	<0.0001	11.24	<0.0001	17.53	<0.0001	11.8	<0.0001
Lower breadth in tolerance	4.78	0.0004	2.13	0.05	9.30	<0.0001	7.80	<0.0001

Each treatment in each season had a sample size of eight fish and DF = 14 for each test

Table 4 Seasonal change in CT$_{max}$, CT$_{min}$, acclimatization temperature, and acclimatization response ratios (AZRR) and thermal safety margin (TSM) for yellowfin mojarra, schoolmaster snapper, checkered puffer, and bonefish

Variable	Yellowfin mojarra	Schoolmaster snapper	Checkered puffer	Bonefish
ΔCT$_{max}$ (°C)	3.6	5.3	3.1	2.7
ΔT (°C)	5.8	5.2	6.6	5.3
AZRR (upper)	0.62	1.02	0.47	0.51
TSM (upper)	−2.0	0.5	−1.4	−4.9
ΔCT$_{min}$ (°C)	4.3	3.6	6.6	3.5
ΔT (°C)	5.1	5.7	5.3	5.7
AZRR (lower)	0.84	0.63	1.25	0.61
TSM (lower)	−0.2	−0.1	0.8	0.4
Total AZRR	1.46	1.65	1.72	1.12

The change in temperature = acclimatization temperature in the summer − acclimatization temperature in the winter. Change in CT$_{max}$ = CT$_{max}$ in the summer − CT$_{max}$ in the winter. Change in CT$_{min}$ = CT$_{min}$ in the summer − CT$_{min}$ in the winter. Each treatment in each season had a sample size of eight fish

Conversely, CT$_{min}$ for yellowfin mojarra was approximately 4 °C lower in winter than in summer, and the lower breadth in tolerance (i.e., acclimatization temperature—CT$_{min}$) of fish in winter (11.2 °C) was almost 4 °C smaller relative to summer (15.5 °C). The thermal scope (summer = 26.2 °C; winter = 25.4 °C) did not differ significantly between seasons for mojarra. The maximum environmental temperature of 43 °C in the nearshore environment exceeded the summer CT$_{max}$ of yellowfin mojarra by 2 °C resulting in a negative upper TSM. A minimum environmental temperature of 11 °C was 0.2 °C cooler than the winter CT$_{min}$ of yellowfin mojarra resulting in a negative lower TSM. Yellowfin mojarra had an upper and lower AZRRs intermediate to other species in this study (Table 4).

Checkered puffer

The thermal scope of checkered puffers was smaller in summer (24.9 °C) compared to winter (28.3 °C; Fig. 1b; Table 3). CT$_{max}$ for checkered puffers was 3 °C higher in summer compared to winter, and the upper breadth in tolerance of checkered puffers in summer (11.2 °C) was 3.5 °C smaller relative to winter (14.7 °C). CT$_{min}$ was 6 °C lower in winter than in summer, and the lower breadth in tolerance in the summer (11 °C) was 1 °C smaller relative to

the winter (12 °C). The maximum environmental temperature of 43 °C in the nearshore environment exceeded the summer CT$_{max}$ of checkered puffers by more than 1 °C resulting in a negative upper TSM. Checkered puffers demonstrated a winter CT$_{min}$ that was 0.8 °C cooler than the minimum environmental temperature of 11 °C giving checkered puffer the most positive lower TSM relative to other species. Checkered puffers had the smallest upper AZRR and the largest lower AZRR relative to all species (Table 4).

Schoolmaster snapper

The thermal maxima and minima of schoolmaster snapper differed significantly across seasons, with CT$_{max}$ approximately 5 °C higher in summer relative to winter. Thermal scope for schoolmaster snapper was greater in the summer (28.6 °C) compared to the winter (27.1 °C; Fig. 1c; Table 3). The upper breadth in tolerance of schoolmaster snapper was not significantly different across seasons (~12 °C). CT$_{min}$ values were over 4 °C lower in the winter relative to the summer, and the lower breadth in tolerance in winter (11.2 °C) was almost 3 °C smaller compared to summer (14 °C). The summer CT$_{max}$ of schoolmaster snapper exceeded the maximum environmental temperature of

43 °C by half a degree resulting in the only positive upper TSM. The winter CT_{min} was higher than the minimum temperature (11 °C) observed in the nearshore environment, resulting in a negative lower TSM. Schoolmaster snapper had the largest upper AZRR and an intermediate lower AZRR relative to all species (Table 4).

Bonefish

The thermal scope of bonefish was lower in the summer (24 °C) relative to the winter (24.7 °C), and CT_{max} was almost 3 °C higher in summer compared to winter (Fig. 1d; Table 3). Moreover, the upper breadth in tolerance of bonefish in summer (8.8 °C) was almost 3 °C smaller relative to winter (11.6 °C). Additionally, the lower breadth in tolerance of bonefish in winter (13.1 °C) was more than 2 °C smaller relative to summer (15.3 °C). The maximum environmental temperature of 43 °C in the nearshore environment exceeded the summer CT_{max} of bonefish by almost 5 °C resulting in the largest negative upper TSM. The CT_{min} of bonefish was almost half a degree lower than the coolest water temperature of 11 °C in the nearshore environment resulting in a positive lower TSM. Bonefish had an intermediate upper AZRR and the smallest lower AZRR relative to all species (Table 4).

Discussion

Quantifying the thermal tolerance of marine fishes, and identifying how those tolerances change across seasons, is important for predicting the physiological vulnerability of fish to the more extreme climates of the future (Gunderson and Stillman 2015). Relative to other tropical/subtropical marine species, the resident nearshore fishes in this study had some of the highest CT_{max} reported; the critical thermal maximum for checkered puffer, yellowfin mojarra, and schoolmaster snapper in the summer acclimatized to 30.4, 30, and 31 °C was 41.6, 41.0, and 43.5 °C, respectively. In comparison, pink cardinalfish, *Apogon pacifici*, that typically inhabit thermally stable coral reef environments exhibit a critical thermal maximum of approximately 35 °C when acclimated to a temperature of 26.5 °C (Mora and Ospina 2001), but this estimate may be high due to a lower heating rate of 1 °C h^{-1} relative to the 0.18 °C min^{-1} used in this study. Alternatively, bullseye puffer fish, *Sphoeroides annulatus*, typically inhabit thermally dynamic nearshore ecosystems and demonstrated a critical thermal maximum that exceeded 40 °C when acclimated to a temperature of 28 °C (Reyes et al. 2011), a thermal maximum that more closely matched that of the species in the current study. This estimate of CT_{max} may be high due to a higher heating rate of 1 °C min^{-1} relative to the 0.18 °C min^{-1}

used in this study. The eurythermal sheepshead minnow, *Cyprinodon variegatus*, is commonly found in tidal pools, an environment that experiences extreme temperatures and has a higher thermal tolerance of 45.1 °C when acclimatized to 37–42 °C at heating rate 0.1 °C min^{-1} (similar to the rate used in this study; Bennett and Beitinger 1997). An over-estimate of CT_{max} may occur if the rate of warming occurs too fast (e.g., 1 °C min^{-1}) due to a lag in temperature change or too slow (e.g., 1 °C h^{-1}) due to thermal acclimation during the assay, with 0.3 °C min^{-1} being the recommend standard for CT_{max} assays (Beitinger et al. 2000). In this study, the warming rate of 0.2 °C min^{-1} was slightly below the recommend warming rate, which may have resulted in an underestimate of CT_{max} for these nearshore fishes. Similarly, acclimation temperature can play an important role in determining the thermal tolerance of fishes, with elevated acclimation temperatures resulting in an increase in CT_{max} (Beitinger and Bennett 2000). Lastly, life stage can influence thermal tolerance limits, with juvenile fish experiencing higher CT_{max} relative to adults (Pörtner and Farrell 2008; Komoroske et al. 2014). Collectively, comparing thermal tolerance across species and ecosystems can be difficult because of differences in warming rate, acclimation temperature, and life stage across studies, but it appears that the critical tolerance limits of fishes in the thermally dynamic nearshore environment, especially resident species, more closely resemble the limits of fish from extreme environments (e.g., tidal rock pools) than from more thermally stable environments (e.g., coral reefs).

Thermal scope is defined as the range of temperatures in which an organism can persist, including passive anaerobic existence (Pörtner and Farrell 2008). Tropical species were previously thought to have a narrow thermal scope that will make them less tolerant of future climate change relative to species from temperate environments (Pörtner and Farrell 2008; but see Seebacher et al. 2014). Recent data, however, suggest that there may be little difference in thermal scope between temperate (28.3 °C) and tropical fish species (25.9 °C; Sunday et al. 2011). In the current study, thermal scope for all species ranged from 24 to 28.6 °C, indicating that these species can cope with a wide range of environmental temperatures. When all nearshore fishes are considered together, summer CT_{max} increased by 3–5 °C relative to winter, and winter CT_{min} decreased by 3–6 °C relative to the summer, demonstrating plasticity in thermal scope across seasons, with thermal scope typically being narrower in the summer relative to the winter. Indeed, temperatures are variable across seasons in the nearshore environment, with the mean temperature in the winter of 21.2 °C increasing by almost 10 °C to a summer temperature of 30.3 °C (Shultz et al. 2014). The range of thermal scopes observed in nearshore fishes in this study can be

found in both tropical and temperate environments (Sunday et al. 2011), indicating that nearshore fishes may be more tolerant to climate change than previously expected (i.e., a mean increase of 2 °C in the next 100 years above mean environmental temperatures is within the thermal scope of nearshore fishes).

The acclimatization responses (i.e., the magnitude of a species' ability to acclimatize to new thermal environments), as well as breadth in tolerance are valuable when evaluating which species across and within ecosystems will be most at risk to climate change. Based on acclimation temperatures and CT_{max} data, marine Crustacea (maximum = 0.35) found in the intertidal zone in temperate climates, and the Mexican bullseye puffer fish, *Sphoeroides annulatus* (maximum = 0.38) found in the nearshore environments in subtropical climates have some of the highest AZRR scores reported in the literature (Hopkin et al. 2006; Reyes et al. 2011). Surprisingly, all of the upper and lower AZRR scores for nearshore fishes in this study were typically greater than 0.60, a value greater than many previously reported AZRR scores for fish (Gunderson and Stillman 2015), suggesting that these fish have a relatively high capacity to acclimatize to thermal conditions. This enhanced ability to acclimatize to new thermal environments (i.e., phenotypic plasticity) has previously been attributed to mechanisms such as an increase in heat shock proteins, stimulation of the cellular stress response, or improved cardiorespiratory function (Fader et al. 1994; Eliason et al. 2011; Jayasundara and Somero 2013; Feidantsis et al. 2013). Within the nearshore ecosystem, bonefish had the lowest total AZRR score (combined upper and lower AZRR scores) of 1.12 relative to other fish species (1.46–1.72), indicating a limited ability to acclimatize to variable thermal landscapes. Similarly, bonefish demonstrate a lower breadth in tolerance limit in the summer (8.8 °C) relative to checkered puffer, schoolmaster snapper, and yellowfin mojarra (11–12 °C), which suggests this fish is more at risk to mean and extreme increases in temperature in the next 100 years relative to other species in this study. Overall, nearshore fishes may have a high capacity to acclimatize to a variable thermal landscape in the future relative to fish species studied to date (Gunderson and Stillman 2015), but the capacity to acclimatize is life stage and/or species specific in the nearshore ecosystem with bonefish having the smallest capacity.

Fish that live near their thermal maximum/minimum (i.e., small TSM) are likely to be more susceptible to a variable climate in the future (e.g., cold snaps and heat waves) if animals should experience temperatures outside critical limits (Somero 2010). Even relatively short-lived extremes in temperature can result in a restructuring of fish communities and biogeographical distributions (Wernberg et al. 2012; Smale and Wernberg 2013). For example, damselfish,

Acanthochromis polyacanthus, found in the tropical coral reef environment exposed to an elevated temperature of 34 °C, just 3 °C above ambient conditions, for a relatively short period of time (maximum 14 days) were pushed beyond their physiological limits, resulting in 100 % mortality (Rummer et al. 2013). Similarly, an extended cold snap in 2010 resulted in high mortality rates for nearshore fish around Florida and has been attributed to the decline in bonefish populations in this area (Szekeres et al. 2014). In this study, present-day maximum and minimum temperatures in the nearshore environment are approximately equal to or exceed the thermal tolerance limits of the fish in this study, making TSM very small or negative. For example, seawater in the nearshore environment during the summer exceeds 40 °C (Shultz et al. 2014), a temperature that surpasses the CT_{max} value for bonefish (38.1 °C) in the summer. Bonefish move into the nearshore environment on an incoming tide and often migrate to deeper cooler waters on the outgoing tide, potentially using these areas as thermal refuge (Murchie et al. 2013). Unfortunately, sea surface temperatures are expected to increase by 0.3–2 °C over the next 100 years due to climate change (IPCC 2013), and heat waves are expected to increase in both frequency and intensity (Coumou and Rahmstorf 2012). This increase in both mean and extreme temperatures has potential to restrict available thermal habitat for bonefish, forcing these fish to spend less time in the nearshore ecosystem and more time in cool refugia. While cool refugia have the potential to alleviate thermal stress, inhabiting these environments may result in missed feeding opportunities and/or elevated mortality due to predation, possibly leading to negative impacts at the population level. The extremes in temperature may have as much, if not more, influence on the distribution and persistence of individual species than mean temperatures (Parmesan et al. 2000; Sunday et al. 2014). On the whole, extreme temperatures due to climate change have potential to influence the survival and/or distribution of nearshore species, and a gradual increase in temperature of 2 °C in the next 100 years will restrict some of the available thermal habitats of these species.

Current mean summer temperatures in the nearshore environment (30.3 °C) fall below the critical thermal maximum of the most sensitive species, bonefish (CT_{max} = 38.1 °C). The IPCC's worst-case thermal scenario predicts that sea surface temperatures will increase by 2 °C in the next 100 years, and push maximum temperatures beyond the TSM of all nearshore fish in this study, including the schoolmaster snapper that has the largest present-day TSM of 0.5 °C. Moreover, nearly all species in this study had relatively large negative upper TSM values in summer relative to the winter, indicating that extreme temperatures associated with heat waves in the summer will likely exceed thermal limits of these fish more frequently than cold snaps

in the winter. This study, however, did not evaluate the phenotypic plasticity of fish to thermal limits within a season which may be an interesting research path to follow in the future now that it has been established that nearshore fish can acclimatize to thermal environments across seasons. This research will be particularly fruitful in the summer when nearshore fishes are most at risk due to small upper breadth in tolerance and TSM relative to the winter.

Altered thermal regimes have the potential to increase mortality, alter habitat choice, constrict the range of species, and alter food web dynamics (Pörtner and Farrell 2008). The possibility of species in the nearshore environment being able to genetically adapt to elevated temperatures is likely small due to long generation times (e.g., bonefish maximum age 20 years) and delayed maturation (e.g., bonefish mature after ~3 years), although most basic life history traits of many species in this ecosystem have not been described. Alternatively, the ability to acclimatize to new thermal environments and proximity to their thermal limits will likely play a larger role in structuring nearshore ecosystems the future. Fishes with a limited ability to acclimatize and that inhabit thermal environments in close proximity to their limits will likely be most at risk as the oceans warm (Madeira et al. 2012). Specifically, nearshore fishes may be forced to migrate to cooler water (e.g., deeper water or cooler microhabitats; Huey and Tewksbury 2009), adapt to an increase in temperature (Hofmann and Todgham 2010), or a combination of these options (Pörtner and Farrell 2008). The degree that each species adopts one or a combination of these strategies will depend on both abiotic and biotic variables. For example, checkered puffer and yellowfin mojarra both have negative upper TSM values under present-day conditions, and environmental temperatures will likely exceed the thermal tolerance of both species more frequently in the future. Checkered puffer may opt to migrate into cooler and potentially predator-rich environments because of its anti-predator defenses (e.g., body armor, toxic), while yellowfin mojarra may need to adapt to temperature extremes because of a lack of anti-predator defenses. Overall, perturbations in thermal conditions because of climate change will alter fish communities in the nearshore environment, a critical nursery habitat for many marine fishes. Species with positive TSM that are capable of acclimatizing to new thermal environments (e.g., schoolmaster snapper) will likely persist in these systems, while relatively intolerant species (e.g., bonefish) may inhabit these systems less frequently or will be absent in the future.

Compliance with ethical standards

References

Barbier EB, Hacker SD, Kennedy C et al (2011) The value of estuarine and coastal ecosystem services. Ecol Monogr 81:169–193. doi:10.1890/10-1510.1

Beitinger TL, Bennett WA (2000) Quantification of the role of acclimation temperature in temperature tolerance of fishes. Environ Biol Fishes 58:277–288. doi:10.1023/A:1007618927527

Beitinger TL, Bennett WA, Mccauley RW (2000) Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Environ Biol Fishes 58:237–275. doi:10.1023/A:1007676325825

Bennett WA, Beitinger TL (1997) Temperature tolerance of the sheepshead minnow, *Cyprinodon variegatus*. Copia 1:77–87. doi:10.2307/1447842

Chipps SR, Clapp DF, Wahl DH (2000) Variation in routine metabolism of juvenile muskellunge: evidence for seasonal metabolic compensation in fishes. J Fish Biol 56:311–318. doi:10.1111/j.1095-8649.2000.tb02108.x

Claussen DL (1977) Thermal acclimation in ambystomatid salamanders. Comp Biochem Physiol Part A Mol Integr Physiol 58:333–340. doi:10.1016/0300-9629(77)90150-5

Coumou D, Rahmstorf S (2012) A decade of weather extremes. Nat Clim Chang 2:491–496. doi:10.1038/NCLIMATE1452

Deutsch CA, Tewksbury JJ, Huey RB et al (2008) Impacts of climate warming on terrestrial ectotherms across latitude. Proc Natl Acad Sci 105:6668–6672. doi:10.1073/pnas.0709472105

Duarte H, Tejedo M, Katzenberger M et al (2012) Can amphibians take the heat? Vulnerability to climate warming in subtropical and temperate larval amphibian communities. Glob Chang Biol 18:412–421. doi:10.1111/j.1365-2486.2011.02518.x

Eliason EJ, Clark TD, Hague MJ et al (2011) Differences in thermal tolerance among sockeye salmon populations. Science 332:109–112. doi:10.1126/science.1199158

Evans DO (1984) Temperature independence of the annual cycle of standard metabolism in the pumpkinseed. Trans Am Fish Soc 113:494–512. doi:10.1577/1548-8659(1984)113<494:TIOTAC>2.0.CO;2

Fader SC, Yu Z, Spotila JR (1994) Seasonal variation in heat shock proteins (hsp70) in stream fish under natural conditions. J Therm Biol 19:335–341. doi:10.1016/0306-4565(94)90070-1

Fangue N, Bennett W (2003) Thermal tolerance responses of laboratory-acclimated and seasonally acclimatized Atlantic stingray, *Dasyatis sabina*. Copeia 2:315–325. doi:10.1643/0045-8511(2003)003[0315:TTROLA]2.0.CO;2

Feidantsis K, Antonopoulou E, Lazou A et al (2013) Seasonal variations of cellular stress response of the gilthead sea bream (*Sparus aurata*). J Comp Physiol B 183:625–639. doi:10.1007/s00360-012-0735-y

Ghalambor CK, Huey RB, Martin PR et al (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integr Comp Biol 46:5–17. doi:10.1093/icb/icj003

Gunderson AR, Stillman JH (2015) Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. Proc R Soc B Biol Sci 282:20150401. doi:10.1098/rspb.2015.0401

Hartley HO (1950) The maximum F-ratio as a short-cut test for heterogeneity of variance. Biometrika 37:308–312. doi:10.2307/2332383

Hofmann GE, Todgham AE (2010) Living in the now: physiological mechanisms to tolerate a rapidly changing environment. Annu Rev Physiol 72:127–145. doi:10.1146/annurev-physiol-021909-135900

Hofmann GE, Barry JP, Edmunds PJ et al (2010) The effect of ocean acidification on calcifying organisms in marine ecosystems: an organism-to-ecosystem perspective. Annu Rev Ecol Evol Syst 41:127–147. doi:10.1146/annurev.ecolsys.110308.120227

Hopkin RS, Qari S, Bowler K et al (2006) Seasonal thermal tolerance in marine Crustacea. J Exp Mar Biol Ecol 331:74–81. doi:10.1016/j.jembe.2005.10.007

Huey RB, Tewksbury JJ (2009) Can behavior douse the fire of climate warming? Proc Natl Acad Sci 106:3647–3648. doi:10.1073/pnas.0900934106

IPCC (2013) Climate change 2013: The physical basis. Contribution of working group 1 to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Jayasundara N, Somero GN (2013) Physiological plasticity of cardiorespiratory function in a eurythermal marine teleost, the longjaw mudsucker, *Gillichthys mirabilis*. J Exp Biol 216:2111–2121. doi:10.1242/jeb.083873

Kerr RA (2011) Humans are driving extreme weather; time to prepare. Science 334:1040. doi:10.1126/science.334.6059.1040

Knutson TR, McBride JL, Chan J et al (2010) Tropical cyclones and climate change. Nat Geosci 3:157–163. doi:10.1038/NGEO779

Komoroske LM, Connon RE, Lindberg J et al (2014) Ontogeny influences sensitivity to climate change stressors in an endangered fish. Conserv Physiol. doi:10.1093/conphys/cou008

Lam K, Tsui T, Nakano K, Randall DJ (2006) Physiological adaptations of fishes to tropical intertidal environments. In: Val AL, De Almeida-Val VMF, Randall DJ (eds) Fish physiology: the physiology of tropical fishes, vol 21. Academic Press Inc, London, pp 501–581

Madeira D, Narciso L, Cabral HN, Vinagre C (2012) Thermal tolerance and potential impacts of climate change on coastal and estuarine organisms. J Sea Res 70:32–41. doi:10.1016/j.seares.2012.03.002

Magozzi S, Calosi P (2014) Integrating metabolic performance, thermal tolerance, and plasticity enables for more accurate predictions on species vulnerability to acute and chronic effects of global warming. Glob Chang Biol 21:181–194. doi:10.1111/gcb.12695

Mora C, Ospina AF (2001) Tolerance to high temperatures and potential impact of sea warming on reef fishes of Gorgona Island (tropical eastern Pacific). Mar Biol 139:765–769. doi:10.1007/s002270100626

Murchie KJ, Danylchuk SE, Pullen CE et al (2009) Strategies for the capture and transport of bonefish, *Albula vulpes*, from tidal creeks to a marine research laboratory for long-term holding. Aquac Res 40:1538–1550. doi:10.1111/j.1365-2109.2009.02255.x

Murchie KJ, Cooke SJ, Danylchuk AJ et al (2011) Thermal biology of bonefish (*Albula vulpes*) in Bahamian coastal waters and tidal creeks: an integrated laboratory and field study. J Therm Biol 36:38–48. doi:10.1016/j.jtherbio.2010.10.005

Murchie KJ, Cooke SJ, Danylchuk AJ et al (2013) Movement patterns of bonefish (*Albula vulpes*) in tidal creeks and coastal waters of Eleuthera, The Bahamas. Fish Res 147:404–412. doi:10.1016/j.fishres.2013.03.019

Nilsson GE, Crawley N, Lunde IG, Munday PL (2009) Elevated temperature reduces the respiratory scope of coral reef fishes. Glob Chang Biol 15:1405–1412. doi:10.1111/j.1365-2486.2008.01767.x

NOAA (2010) National Oceanic and Atmospheric Administration's National Weather Source. National Data Buoy Center. http://www.ndbc.noaa.gov/N

Norin T, Malte H, Clark TD (2014) Aerobic scope does not predict the performance of a tropical eurythermal fish at elevated temperatures. J Exp Biol 217:244–251. doi:10.1242/jeb.089755

Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. Bull Am Meteorol Soc 81:443–450. doi:10.1175/1520-0477(2000)081<0443:IOEWAC>2.3.CO;2

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915. doi:10.1126/science.1111322

Poloczanska ES, Brown CJ, Sydeman WJ et al (2013) Global imprint of climate change on marine life. Nat Clim Chang 3:919–925. doi:10.1038/nclimate1958

Pörtner HO (2002) Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comp Biochem Physiol A: Mol Integr Physiol 132:739–761. doi:10.1016/S1095-6433(02)00045-4

Pörtner HO, Farrell AP (2008) Physiology and climate change. Science 322:690–692. doi:10.1126/science.1163156

Pörtner HO, Peck MA (2010) Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. J Fish Biol 77:1745–1779. doi:10.1111/j.1095-8649.2010.02783.x

Reyes I, Díaz F, Re AD, Pérez J (2011) Behavioral thermoregulation, temperature tolerance and oxygen consumption in the Mexican bullseye puffer fish, *Sphoeroides annulatus* Jenyns (1842), acclimated to different temperatures. J Therm Biol 36:200–205. doi:10.1016/j.jtherbio.2011.03.003

Roessig JM, Woodley CM, Cech JJ, Hansen LJ (2005) Effects of global climate change on marine and estuarine fishes and fisheries. Rev Fish Biol Fish 14:251–275. doi:10.1007/s11160-004-6749-0

Rummer JL, Couturier CS, Stecyk JAW et al (2013) Life on the edge: thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures. Glob Chang Biol 20:1055–1066. doi:10.1111/gcb.12455

Seebacher F, White CR, Franklin CE (2014) Physiological plasticity increases resilience of ectothermic animals to climate change. Nat Clim Chang 5:61–66. doi:10.1038/nclimate2457

Shultz AD, Zuckerman ZC, Stewart HA, Suski CD (2014) Seasonal blood chemistry response of sub-tropical nearshore fishes to climate change. Conserv Physiol 2:1–12. doi:10.1093/conphys/cou028.Introduction

Smale DA, Wernberg T (2013) Extreme climatic event drives range contraction of a habitat-forming species. Proc R Soc B Biol Sci 280:20122829. doi:10.1098/rspb.2012.2829

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. W.H Freeman, New York

Somero GN (2010) The physiology of climate change: How potentials for acclimatization and genetic adaptation will determine "winners" and "losers". J Exp Biol 213:912–920. doi:10.1242/jeb.037473

Somero GN (2012) The physiology of global change: linking patterns to mechanisms. Annu Rev Mar Sci 4:39–61. doi:10.1146/annurev-marine-120710-100935

Stillman JH (2003) Acclimation capacity underlies susceptibility to climate change. Science 301:65. doi:10.1126/science.1083073

Sunday JM, Bates AE, Dulvy NK (2011) Global analysis of thermal tolerance and latitude in ectotherms. Proc R Soc B Biol Sci 278:1823–1830. doi:10.1098/rspb.2010.1295

Sunday JM, Bates AE, Kearney MR et al (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proc Natl Acad Sci USA 111:5610–5615. doi:10.1073/pnas.1316145111

Szekeres P, Brownscombe JW, Cull F et al (2014) Physiological and behavioural consequences of cold shock on bonefish (*Albula vulpes*) in The Bahamas. J Exp Mar Biol Ecol 459:1–7. doi:10.1016/j.jembe.2014.05.003

Trenberth KE, Fasullo JT (2012) Climate extremes and climate change: the Russian heat wave and other climate extremes of 2010. J Geophys Res Atmos. doi:10.1029/2012JD018020

Valiela I, Bowen JL, York JK (2001) Mangrove forests: one of the world's threatened major tropical environments. Bioscience 51:807–815. doi:10.1641/0006-3568(2001)051[0807:MFOOTW]2.0.CO;2

Vanlandeghem MM, Wahl DH, Suski CD (2010) Physiological responses of largemouth bass to acute temperature and oxygen stressors. Fish Manag Ecol 17:414–425. doi:10.1111/j.1365-2400.2010.00740.x

Wernberg T, Smale DA, Tuya F et al (2012) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Chang 3:78–82. doi:10.1038/nclimate1627