



# Thermal responses of juvenile squaretail mullet (*Liza vaigiensis*) and juvenile crescent terapon (*Terapon jarbua*) acclimated at near-lethal temperatures, and the implications for climate change

John Eme<sup>a,\*</sup>, Theresa F. Dabruzzi<sup>b</sup>, Wayne A. Bennett<sup>b</sup>

<sup>a</sup> Department of Biological Sciences, University of North Texas, Denton, TX 76203-5017, USA

<sup>b</sup> Department of Biology, University of West Florida, Pensacola, FL 32514-5750, USA

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## ABSTRACT

The negative effects of climate alteration on coral reef fishes receive ever increasing attention; however, implications of rising sea temperatures on fishes inhabiting marine nursery environments are poorly understood. We used critical thermal methodology to quantify critical thermal maxima (CT<sub>maxima</sub>) of juvenile squaretail mullet (*Liza vaigiensis*) and juvenile crescent terapon (*Terapon jarbua*) captured from shallow seagrass nursery areas around Hoga Island, southeast Sulawesi, Indonesia. We tested the hypothesis that these distantly related fishes, when acclimated to cycling temperatures, would display higher CT<sub>maxima</sub> than groups acclimated at constant temperatures. Groups of mullet acclimated to a constant temperature of 37 °C and temperature cycles of 35 to 39 °C or 37 to 41 °C displayed statistically similar mean CT<sub>maxima</sub> of 44.7, 44.4 and 44.8 °C, respectively. Likewise, terapon acclimated at temperature cycles of 37 to 40 °C did not display a higher CT<sub>maxima</sub> than fish acclimated at a constant temperature of 37 °C, with both acclimation groups' mean CT<sub>maxima</sub> equal to 43.8 °C. Acclimation to higher cycling temperatures did not result in significant upper temperature tolerance acquisition for either species; however, mullet values were significantly higher than those seen in terapon ( $P < 0.0001$ ). These data suggest that mullet and terapon will not suffer direct thermal effects should shallow nursery temperature increases be marginally higher than 1–2 °C above ~27 °C, and they provide evidence that the upper thermal tolerance of fishes inhabiting shallow seagrass and mangrove areas can approach the biokinetic limits for vertebrate life. Tropical marine fishes inhabiting fringing nursery environments may have the upper thermal tolerance necessary to endure substantial increases in sea temperatures.

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## 1. Introduction

Temperate fishes have been considered especially vulnerable to changing climate conditions (McCarty, 2001; Xenopoulos et al., 2005); however, increasing water temperatures may also threaten shallow-water marine fishes inhabiting nursery environments, like tropical mangroves and seagrass beds. Recent studies from the equatorial Indo-Pacific suggest that hyperthermicity is more common among fishes than previously believed. Nearly 70% of field acclimated juvenile fishes (44 species acclimated to ~27 °C) inhabiting tropical mangrove, seagrass and tidepool habitats around a single island, Hoga Island (05° 27.53 S, 123° 46.33E), southeast Sulawesi, Indonesia, exhibit critical thermal maximum values at or above 40 °C (Bennett, 2010; critical thermal maximum – CT<sub>maximum</sub> – upper thermal tolerance). By comparison, only 3% of subtropical and

temperate North American fishes demonstrate similar thermal tolerance levels (Beitinger et al., 2000), and extreme high temperature tolerance in fishes was thought to be limited to a relatively few groups living in novel hyperthermal environments. For example, Pupfishes (Cyprinodontidae) inhabiting mangroves and tidepools exhibit CT<sub>maxima</sub> as high as 45.2 °C, the highest whole-body temperatures ever measured in a living vertebrate and the biokinetic limit for vertebrate life (Heath et al., 1993; Bennett and Beitinger, 1997). Given that current thermal tolerance paradigms are based largely on data from fishes of the Americas (Houston, 1982; Lutterschmidt and Hutchison, 1997; Beitinger et al., 2000), excluding the much more biodiverse waters of the Indo-Pacific, it is not surprising that our understanding of tropical fish responses to temperature change is rudimentary (Wilson et al., 2010).

Tropical, shallow marine habitats, such as seagrasses and mangroves, are frequently subjected to rapid and extreme temperature increases (Taylor et al., 2005; Eme and Bennett, 2009). Grand mean monthly high temperatures from 1981 to 2004 in the Indo-Pacific were ~32 °C, approximately 5 °C higher than mean sea surface temperatures (NOAA; 35°N to 30°S; see Eme and Bennett, 2009 for

\* Corresponding author at: University of North Texas, Department of Biological Sciences, 1155 Union Circle, #305220, Denton, TX 76203-5017, USA. Tel.: +940 565 2011.

E-mail address: [johneme34@gmail.com](mailto:johneme34@gmail.com) (J. Eme).

URL: <http://web.mac.com/jeme/Site/Home.html>.

Discussion). Nevertheless, shallow marine habitats in the Indo-Pacific are biodiverse and important nurseries for suitably adapted fishes. Thermal conditions within shallow nurseries are likely to be impacted by the 1–2 °C increase in mean sea surface temperatures predicted for the region over the next 50 years (27 °C to 28/29 °C; IPCC, 2007), perhaps to a greater degree than adjacent coral reefs, a generally deeper and more stable marine environment.

The negative effects of temperature alteration on coral reef fishes are relatively well studied (e.g. Menasveta, 1981; Mora and Ospina, 2001; Munday et al., 2008); however, implications of rising sea temperatures on fishes inhabiting fringing nursery environments are poorly documented (Wilson et al., 2010). It is assumed that juvenile fishes living at cooler latitudes should have some capacity to adapt to changing thermal conditions (Munday et al., 2008), but it is unclear if tropical populations possess sufficient acclimation capacity to accommodate further temperature increase. In the present study, we test the hypothesis that two distantly related fishes (Yagishita et al., 2009; Blasie Li, personal communication), juvenile squaretail mullet, *Liza vaigiensis* (Quoy and Gaimard, 1824–1825) and juvenile crescent terapon, *Terapon jarbua* (Forsskal, 1775), acclimated to cycling temperatures approaching 40 °C will display higher CTmaxima than groups acclimated to a lower constant temperature of 37 °C. Both fish are hyperthermal specialists (Eme and Bennett, 2009; Bennett, 2010) that spend their first year in shallow, protected seagrass and mangrove nurseries (Hiatt and Strasburg, 1960; Pauly et al., 1996), and as adults make up an important component of commercial and artisanal fisheries throughout coastal Southeast Asia (Myers, 1991; Rainboth, 1996). However, juveniles of both species do not remain in isolated tidepools during daytime low tides, thereby likely avoiding the hottest temperatures (personal observations; Hiatt and Strasburg, 1960; Pauly et al., 1996). Sea surface temperature increases have the potential to adversely affect fish stocks as well as reef biodiversity (Somero, 2010), and it will become increasingly important to answer the question of how juvenile fishes may respond to temperature increases in nursery habitats.

## 2. Materials and methods

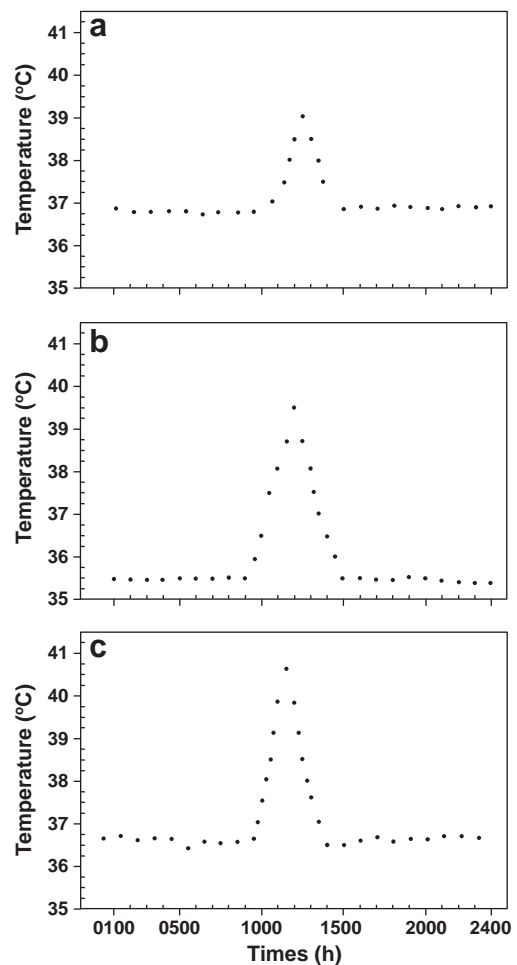
### 2.1. Collection, transport, maintenance and thermal acclimation of fishes

Experiments were conducted during a 10-week expedition to Hoga Island from June to September 2010. Juvenile fishes were collected at low tide from intertidal seagrass sites, transported to the Hoga Marine Research Centre, and transferred into 95-L, biologically filtered holding tanks containing clean seawater at  $27 \pm 1$  °C and  $34.5 \pm 0.5\%$  salinity. Squaretail mullet and crescent terapon were housed separately during holding and acclimation periods and were fed Sera™ Vegetarian Diet flake food, and Ocean Nutrition™ Formula One Marine sinking pellets, respectively. Fishes were fed twice daily until satiated, but were not fed 24 h prior to, or during CTM trials (below). All fish readily accepted food throughout the acclimation period, including shortly after peak temperatures were reached during thermal cycling events.

After a 2 to 3 day holding period, fish were randomly sorted into replicate 17-L acclimation aquaria and assigned to either a constant or cycling temperature treatment. Acclimation aquaria were biological filtered, and 10–15% of water was exchanged per hour via a flow-through seawater system to insure good water quality. Replicate aquaria were suspended (three each) into temperature controlled (200-W, Haile aquarium heater), recirculating 95-L water baths (AZOO powerhead). Water bath temperatures were increased  $1.5 \pm 0.5$  °C day<sup>-1</sup> (mean  $\pm$  SD) from ambient levels ( $\sim 26$  °C) until treatment aquaria reached their assigned constant or low cycle temperatures (monitored with a Fisherbrand® NIST mercury thermometer  $\pm 0.1$  °C). All cycling treatment aquaria were then held at end point temperatures an additional two days, after which they were

exposed to once-daily thermal cycling. Cycles were started each day between 07:00 and 10:00 local time by turning on a 300 W AZOO aquaria heater in the treatment water bath. Water temperatures were always monitored every 15–30 min by a researcher using a Fisherbrand® NIST mercury thermometer ( $\pm 0.1$  °C), and measurements were occasionally supplemented by ThermoChron iButton® temperature logger recordings of cycling temperatures at 3 min intervals ( $\pm 0.5$  °C; Fig. 1). Temperatures in cycled aquaria increased by  $1.5 \pm 0.1$  °C h<sup>-1</sup> until peak cycle temperatures were reached. Peak temperatures were held for an additional 20 min after which heaters were turned off and water temperatures returned to baseline levels over the next 1 to 2 h.

Replicate groups of 4 to 8 squaretail mullet were acclimated at a constant temperature of 37 °C (6 replicates) for 10 d, or exposed to respective temperature cycles of 35–39 °C and 37–41 °C for 7 days (3 replicates each). Due to their aggressive nature, crescent terapon were housed at treatment densities of 2 to 5 fish. Terapon were unable



**Fig. 1.** Representative traces of a typical daily temperature regime (0000–2400 h) for terapon, (a) and mullet (b, c) in cycling temperature acclimation treatments. Points on the graph represent single data points collected at their representative time point. (a) Representative trace of temperature regime, including single temperature cycling event for a replicate aquarium containing terapon in the 37.1–39.7 °C treatment. (b) Representative trace of temperature regime, including single temperature cycling event for a replicate aquarium containing mullet in the 35.5–39.4 °C treatment. (c) Representative trace of temperature regime, including single temperature cycling event for a replicate aquarium containing mullet in the 37.0–40.9 °C treatment. Data were collected  $\pm 0.5$  °C during the temperature cycling event using a ThermoChron iButton® temperature logger, and manually collected  $\pm 0.1$  °C using a calibrated thermometer before and after the cycling event. A 300 W aquarium heater was turned on at the beginning of the temperature cycle (i.e., temperature increase), and it was turned off at the cycle's peak.

to tolerate the higher acclimation cycle used in mullet experiments; a single cycle of 37–41 °C resulted in complete mortality of 15 terapon amongst three replicate aquaria. Terapon were acclimated to only a single constant and cycling treatment – 9 replicates at 37 °C for 10 d and 3 replicates at 37–40 °C for 7 d, respectively.

2.2. Critical thermal maximum determination and statistical comparisons

Following acclimation, critical thermal maximum (CT<sub>maximum</sub>) values were estimated using Critical Thermal Methodology (Cox, 1974; Becker and Genoway, 1979; Paladino et al., 1980; Beitinger et al., 2000). For each CTM trial, fish were placed, one each, into 250-ml Nalgene® beakers filled with clean seawater at the appropriate constant temperature or minimum cycling temperature. CTM trials were conducted between 08:00 and 15:00 local time. Beakers were then suspended within a 20-L recirculating water bath and provided with moderate aeration to prevent thermal stratification. Beaker water temperatures were measured with a certified Fisherbrand® NIST mercury thermometer (±0.1 °C). Temperatures were increased at 0.31 ± 0.05 °C min<sup>-1</sup>, a rate slow enough to track body temperature, but fast enough to prevent thermal acclimation (Cox, 1974; Becker and Genoway, 1979). Temperature increase continued until fish exhibited final loss of equilibrium (LOE), defined as the inability to maintain dorso-ventral orientation for at least 1 min (Beitinger et al., 2000). As fish reached LOE, the beaker temperature was recorded. Fish were immediately removed from the CTM chamber and returned to their acclimation temperature, then weighed (wet mass ± 0.01 g) and measured (standard length ± 0.5 mm). 64% of all fish survived for ≥ 1 h following trials.

Mean LOE values were calculated for each treatment replicate within species, and CT<sub>maximum</sub> of the treatment taken as the grand mean of collective replicates (Cox, 1974). Two-way Analysis of Variance (two-way ANOVA) was used to test for interaction effects of species by mass on CT<sub>maximum</sub>, and CT<sub>maximum</sub> differences between species. Differences between CT<sub>maximum</sub> values within species were tested using one-way ANOVA, followed by Tukey's Studentised Range (TSR) *post-hoc* test.

Throughout the text, means are given ± SD. All statistical decisions were based on α = 0.05. Fish were treated in accordance with protocols approved by the University of West Florida, Animal Care and Use Committee (reference #2010-002).

3. Results

Both squaretail mullet and crescent terapon were exceptionally tolerant of high temperatures, and exhibited mean CT<sub>maxima</sub> values ranging between 43.8 and 44.8 °C depending on acclimation treat-

ment (Table 1). Two-way ANOVA found no significant interaction between species and mass ( $F_{1,3} = 3.79, P = 0.06$ ). Likewise, mass alone had no significant effect on fish CT<sub>maximum</sub> values ( $F_{1,3} = 3.79, P = 0.74$ ). CT<sub>maxima</sub> of squaretail mullet were significantly greater than crescent terapon values ( $F_{1,3} = 3.79, P < 0.0001$ ).

Intraspecific comparisons determined that the CT<sub>maximum</sub> of terapon in the 37 °C acclimation group was not significantly different from terapon in the 37 to 40 °C cycled treatment (one-way ANOVA,  $F_{1,10} = 0.00, P = 0.96$ ), with both groups exhibiting mean CT<sub>maxima</sub> of 43.8 ± 0.3 °C (Table 1). Squaretail mullet did show a statistical difference between treatments (one-way ANOVA,  $F_{2,9} = 6.02, P = 0.02$ ). Mean CT<sub>maximum</sub> of the 37 to 41 °C cycled fish was significantly higher (TSR α = 0.05) than the 35 to 39 °C cycled group (44.8 ± 0.1 and 44.4 ± 0.1 °C, respectively). However, mullet in the constant 37.0 °C acclimation group had an intermediate mean CT<sub>maximum</sub> value of 44.7 ± 0.1 °C that was statistically similar to both mean cycle treatment CT<sub>maxima</sub>.

4. Discussion

Squaretail mullet and crescent terapon exhibit notably high CT<sub>maxima</sub> and survive repeated exposure to extreme high temperatures, values very close to those seen in the most thermally tolerant vertebrates, pupfishes (Bennett and Beitinger, 1997). Fish exposed to cycling thermoperiods typically acclimate to the high cycle temperature (Otto and Gerking, 1973; Threader and Houston, 1983; Feldmeth, 1981; Heath et al., 1993). Mullet and terapon, however, acclimated to the lower cycling temperature, refuting our hypothesis that cycle-acclimated fish would display higher CT<sub>maxima</sub> than those exposed to constant temperatures. Atlantic stingrays (*Dasyatis sabina*) are the only other fish known to show this response, and the acclimation strategy helps stingrays survive winter temperatures that come within a degree of their CT<sub>minimum</sub> (Fangue and Bennett, 2003). While both terapon (Russell and Houston, 1989) and mullet (Harrison and Senou, 1997) have distributions extending into cooler latitudes (~35°N–30°S), the fish probably never encounter freezing temperatures. It seems likely that their acclimatory response is not a cold tolerance adaptation, but rather an artifact of their heat tolerance in which they achieve maximum tolerance at approximately 37 °C, with no additional gains made as ambient temperatures continue to rise.

Exceptionally high CT<sub>maxima</sub> afford mullet and terapon a significant measure of protection against changing habitat conditions, a situation not unique to these two species. Sixty-five juvenile fish species representing nine orders from Hoga's nursery areas, exhibit field acclimatized CT<sub>maxima</sub> between 39 and 43 °C (Bennett, 2010). Despite diverse independent origins across taxa (Chen et al., 2003; Li et al., 2009; Yagishita et al., 2009), fishes may share a common suite of physiological adaptations allowing them to survive periodic exposure

Table 1

Standard length (Length), mass, acclimation treatment details, and critical thermal maximum (CT<sub>max</sub>) for juvenile squaretail mullet (*Liza vaigiensis*) and juvenile crescent terapon (*Terapon jarbua*) used in upper thermal tolerance trials. Acclimation treatment groups are organized by type of temperature exposure (Type – cycled or constant temperature), low (T<sub>LOW</sub>) and peak (T<sub>PEAK</sub>) temperatures used in daily cycling acclimation, number of days fish were held at acclimation conditions (Duration), and the number of treatment replications (Rep). T<sub>PEAK</sub> represents the grand mean temperature of replicate aquaria during the 20-min high temperature holding period, and T<sub>LOW</sub> represents the grand mean temperature of replicate aquaria prior to the beginning of the daily temperature cycle. Critical thermal maxima are compared within species, and like superscripts denote groups that do not differ significantly (TSR following one-way ANOVA, α = 0.05).

Length (cm)	Mass (g)	Acclimation treatment					CT <sub>max</sub> (°C)			
		Type	T <sub>LOW</sub> (°C)	Mean ± SD	T <sub>PEAK</sub> (°C)	Mean ± SD	Duration (d)	N	Rep	Mean ± SD
Squaretail mullet ( <i>Liza vaigiensis</i> )										
2.57 ± 0.22	0.57 ± 0.17	Cycled	35.5 ± 0.6		39.4 ± 0.5		7	21	3	44.4 ± 0.1 <sup>b</sup>
2.58 ± 0.30	0.55 ± 0.12	Cycled	37.0 ± 1.0		40.9 ± 1.6		7	15	3	44.8 ± 0.1 <sup>a</sup>
2.60 ± 0.28	0.67 ± 0.25	Constant	37.0 ± 0.1				10	35	6	44.7 ± 0.1 <sup>ab</sup>
Crescent terapon ( <i>Terapon jarbua</i> )										
4.21 ± 0.43	2.20 ± 0.90	Cycled	37.1 ± 0.7		39.7 ± 0.7		7	14	3	43.8 ± 0.3 <sup>a</sup>
4.35 ± 0.40	2.64 ± 0.73	Constant	36.7 ± 0.2				10	34	9	43.8 ± 0.3 <sup>a</sup>

to high environmental temperatures (Hochachka and Somero, 2002; Somero, 2010). Exceptional thermal tolerance may be common throughout the biodiverse shallow waters of the Indo-Pacific.

Sea surface temperatures across the tropical Pacific are expected to increase from ~27 °C to ~29 °C this century (IPCC, 2007). While these levels would pose no direct threat to tropical fish survival, other influences such as habitat degradation, changing food availability and altered metabolic requirements could result in population declines and even extirpation of some groups (Eme and Bennett, 2009; Nilsson et al., 2009; Wilson et al., 2010). However, terapon and mullet demonstrate exceptional tolerance to high temperatures, and it seems likely that shallow-water sea surface temperatures would have to be much higher to adversely affect these and other shallow water marine fishes (Eme and Bennett, 2009). In future studies, comparisons of the thermal biology of fishes inhabiting shallow seagrass and mangrove areas versus adjacent deeper patch reef and coral reef habitats may reveal important trends for which species may better mitigate increasing sea temperatures (Eme and Bennett, 2009; Nilsson et al., 2009).

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### Glossary

*CTmaxima*: Critical Thermal Maxima is a dynamic estimation of upper thermal limit  
*LOE*: loss of equilibrium is a non-lethal endpoint for *CTmaxima* trials where the fish cannot maintain dorso-ventral orientation for at least 1 min