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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

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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 (CTmaxima) 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 CTmaxima 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 CTmaxima 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 CTmaxima than fish acclimated at a constant temperature of 37 °C, with both acclimation groups' mean CTmaxima 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.

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 acclimatized 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 – CTmaximum – 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 CTmaxima 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

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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 ± 1 °C and 34.5 ± 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 sated, 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 ± 0.5 °C day^{-1} (mean ± SD) from ambient levels (~26 °C) until treatment aquaria reached their assigned constant or low cycle temperatures (monitored with a Fisherbrand® NIST mercury thermometer ± 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 (± 0.1 °C), and measurements were occasionally supplemented by Thermochron iButton® temperature logger recordings of cycling temperatures at 3 min intervals (± 0.5 °C; Fig. 1). Temperatures in cycled aquaria increased by 1.5 ± 0.1 °C h^{-1} 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

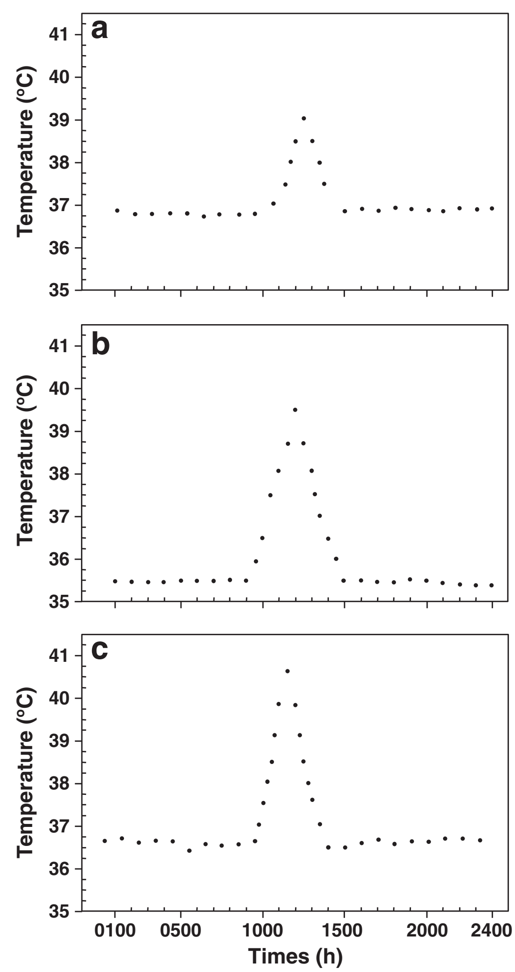

Fig. 1. Representative traces of a typical daily temperature regime (0000–2400 h) for terapon, (a) and mullet (b, c) in cycling temperature acclimation treatments. Points on the graph represent single data points collected at their representative time point. (a) Representative trace of temperature regime, 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 ± 0.5 °C during the temperature cycling event using a Thermochron iButton® temperature logger, and manually collected ± 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.