



Body size and thermal tolerance in tropical gobies



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ABSTRACT

Climatic models have projected an increase in the frequency and intensity of heat waves and cold events over the next century that have the potential to disrupt community dynamics, by reducing resilience of keystone species, such as cleaner fishes. One of the universal responses to global warming, together with shifts in geographic range and phenology, is the reduction of body size across taxonomic groups. As this phenomenon will likely play a major role in shaping communities, we investigate the effect of body size on acute thermal tolerance in cleaner gobies. In this study we set out to test the hypothesis that smaller fishes may be better able to tolerate acute temperature changes in the environment thus making them more resilient during extreme thermal events. We raised cleaner gobies of the genus *Elacatinus* (*E. oceanops* and the dwarf-sized *E. lobeli*) under common garden conditions and tested the effect of inter-individual variation in adult body size on thermal tolerance, using critical thermal methodology. Results from this study show that both species exhibit a limited capacity for acquired thermal tolerance following acclimation. Additionally, the smaller *E. lobeli* was able to tolerate higher and lower temperatures than *E. oceanops*. However, *E. oceanops* showed intraspecific difference in thermal tolerance, with smaller individuals being more thermo-tolerant. The comparison within these two species suggests that body size could have a role in thermo-tolerance and future physiological studies may test a range of sizes to capture the variation in responses of species and populations to temperature stress.

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1. Introduction

Climate change is considered by many researchers to be one of the greatest current threats to biodiversity and ecosystem stability across biota (Bellard et al., 2012; Leadley et al., 2010). Therefore, predicting its impacts at the organismal level has become a major research goal for evolutionary and conservation biologists (Di Santo, 2015; Kappelle et al., 1999; Somero, 2010; Wernberg et al., 2011). Current physical models predict an increase in frequency, duration and magnitude of sudden and rapid thermal fluctuations as a consequence of anthropogenic global warming (Harley et al., 2006; Helmuth et al., 2010; IPCC, 2013; Karl et al., 2011). Most studies looking at the effects of environmental stress on fishes focus on the direct and indirect consequences of increased average temperatures on physiology (for example, Beitinger and Bennett, 2000; Di Santo, 2015; Di Santo and Lobel, 2016; Fry, 1971), but the occurrence of short-term intensive perturbations (e.g. cold fronts, heat waves) also have the potential to disrupt ecosystem stability by eliminating keystone species (Rossi et al., 2013; Sazima et al., 2010; Seebacher et al., 2015). As nearly every physiological process is temperature-sensitive in aquatic ectotherms (Di Santo and

Bennett, 2011a; Fry, 1947; Magnuson et al., 1979; Ohlberger et al., 2012; Schmidt-Nielsen, 1997; Somero, 2010), acute thermal changes are thought to profoundly affect fishes, with consequences for the stability of the whole community (Forster et al., 2012; Gilman et al., 2010; Perry et al., 2005; Sunday et al., 2011). Climatic models project a 2–3 °C increase in average ocean temperatures at low latitudes by the end of the century (IPCC, 2013), and as many tropical fishes are known to live close to their thermal limits (Rummer et al., 2014), they are expected to be particularly sensitive to rapid temperature changes (Seebacher et al., 2015).

Current warming is already correlating with shifts in species distribution, phenology, and reduced body size across marine taxa (Cheung et al., 2012; Daufresne et al., 2009; Genner et al., 2010; Ohlberger et al., 2012; Perry et al., 2005). During past major warming events, both marine and terrestrial organisms showed a tendency to become smaller, suggesting a universal response to climate change (Clark et al., 2012; Daufresne et al., 2009; Gardner et al., 2011), a phenomenon also known as the ‘Lilliput effect’ (Harries and Knorr, 2009; Keller and Abramovich, 2009; Song et al., 2011). In particular, fossil evidence suggests that during the warming phase of the Paleocene-Eocene Thermal Maximum (PETM), the mass of ectotherms shrank by 50–75% (Sheridan and Bickford, 2011). Current warming is occurring at a much faster rate than in previous periods, therefore understanding if a reduction in body size is a likely response to temperature increase

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could be very useful to predict changes in biomass expected for the next century (Angilletta et al., 2004; Gardner et al., 2011; Sheridan and Bickford, 2011).

The Lilliput effect could be explained by the fact that smaller fishes are generally found in low oxygen or marginal environments, and consequently may have an acquired or intrinsic tolerance to acute or chronic temperature changes (Fry and Hart, 1948; Keller and Abramovich, 2009). Nonetheless, demonstrating an increase in acute thermal tolerance in smaller fish has been difficult, as results disagree on the effect of body size on tolerance (for example, Barrionuevo and Femandes, 1995; Ospina and Mora, 2004; Pörtner and Knust, 2007; Recsetar et al., 2012). Many previous studies compared different age classes (for instance, juveniles vs. adults), thus making it difficult to exclude the effect of changing metabolic requirements and sensitivities linked to particular life stages (Recsetar et al., 2012). To overcome these limitations, it is possible to evaluate variations in thermal tolerance of conspecifics or congeners that occupy similar environments but possess different adult sizes (Landry et al., 2007; Ohlberger et al., 2012; Ohlberger et al., 2008; Shields and Underhill, 1993). By testing the effect of body size on acute thermal tolerance in laboratory-controlled settings, it is possible to exclude differences derived by dissimilar acclimation histories and life stages from those resulting from body mass alone (Baumann and Conover, 2011; Di Santo, 2015), although transgenerational effects are known to play a role in stress response throughout development and in adults (Salinas and Munch, 2012).

The Caribbean goby, *Elacatinus lobeli* Randall and Colin, 2009, was considered a dwarf variant of the well-known neon goby, *Elacatinus oceanops* Jordan 1904, until genetic and morphological data supported a species level designation (Randall and Colin, 2009; Taylor and Hellberg, 2006, 2005). The two species are ecologically equivalent; they reside in colonies on shallow live coral heads where they wait to clean potential fish hosts from external parasites (Olivotto et al., 2005; Whiteman and Côté, 2004). They are also morphologically similar except for a difference in coloration and body mass, with *E. oceanops* being larger than *E. lobeli* (Randall and Colin, 2009). These two species also show intraspecific variation in adult body size (Di Santo and Lobel, 2016), therefore they make a good model to test the effect of body size on thermal tolerance. In a previous study, the authors tested the digestive performance of *E. oceanops* and *E. lobeli* at different temperatures and found that the larger gobies have reduced digestion performance at higher temperatures when compared to smaller individuals of the same or sister species (Di Santo and Lobel, 2016). These results seem to support the hypothesis that smaller fishes fare better in warming environments (Twitchett, 2007). As increasing temperature is accompanied by a decrease in dissolved oxygen in the water, and increasing respiratory surfaces is metabolically expensive (Atkinson, 1994; Horne et al., 2015; Forster et al., 2012), larger fishes might suffer from the masking effect of temperature on oxygen availability thus showing greater thermal sensitivity than smaller individuals (Fry, 1947, 1971). In support of this hypothesis, analyses of the correlation between temperature and body size across a wide range of species, from protists to animals, show a strong negative relationship between size and temperature in aquatic species (Atkinson, 1994; Forster et al., 2012) furthering the idea that oxygen supply, thermal sensitivity and body mass are intertwined. In this study, the hypothesis that fishes would exhibit a negative correlation between body size and thermal tolerance was tested in adult cleaner gobies acclimated to a set of temperatures, in 'common garden' conditions.

2. Material and methods

2.1. Holding conditions of experimental animals and thermal profiles

Juvenile *E. lobeli* ($n = 48$) were collected at Wee Wee Caye, Belize (16.76N, 88.14W), while juvenile *E. oceanops* ($n = 48$) were collected in Key Largo, Florida, USA (25.16N, 80.29W). Fishes were divided by

species and randomly assigned to independent tanks, in one of three constant temperature acclimation groups, 20, 24, or 28 °C. All groups were maintained in well aerated and filtered 130-L aquaria, and kept at diel photoperiod of 12 h light: 12 h dark. Water quality in each tank was monitored weekly to test for ammonia, nitrites, and nitrates. Fishes were fed a mixed diet of fresh frozen mysis shrimp and marine flakes twice daily ad libitum throughout the acclimation period but were fasted for 24 h prior to experimentation to ensure measurements were taken while the animals were in post-absorptive state. Temperature was initially set at 24 ± 0.5 °C with a submersible Ebo Jager 50-W aquarium heater. After a two-week period at 24 °C, water temperatures were unchanged, or increased or decreased 0.5 °C per day until reaching acclimation temperatures of 20, 24, and 28 °C, which were then maintained for one year (i.e. until fish reached adult size and thermal tolerance was tested). The upper and lower temperatures were chosen using the chronic thermal tolerance methodology (Beitinger and Bennett, 2000). Briefly, temperature was either decreased or increased 0.5 °C per day to determine the temperature tolerance of cleaner gobies with feeding cessation as the endpoint (Beitinger and Bennett, 2000). The behavior of fishes was observed twice a day and the temperature at which each fish refused food for two consecutive feeding events was recorded, i.e. endpoint of chronic tolerance experiment (Bennett et al., 2000). Chronic upper temperature for *E. lobeli* was 29.7 ± 0.2 °C (range: 28.5–31 °C) while for *E. oceanops* was 29 ± 0.1 °C (range: 28–29.5 °C). The chronic lower temperature for *E. lobeli* was 19.2 ± 0.2 °C (range: 17.5–20 °C) while for *E. oceanops* was 18.9 ± 0.1 °C (range: 18–19.5 °C). Thermal profiles (over a period of about 10 years) at the two locations where fishes were collected were analyzed to determine mean maximum and minimum temperature as well as the average temperatures experienced by these two species (Di Santo and Lobel, 2016). Water thermal data from Wee Wee Caye, Belize were recorded every hour using HOBO temperature loggers (loggers and data were lost between 2008 and 2010 due to a hurricane). Ocean temperature data from the reef at Key Largo, Florida Keys, USA were obtained from NOAA (<http://www.nodc.noaa.gov>).

2.2. Critical thermal methodology

To quantify high and low temperature tolerance, critical thermal maximum (CTMax) and minimum (CTMin) of *E. lobeli* and *E. oceanops* were calculated as the arithmetic mean temperature at which fishes exhibited loss of equilibrium (LOE), defined as the inability to maintain dorsal-ventral posture for 1 min (Cox et al., 1974; Eme and Bennett, 2009; Mora and Ospina, 2002) or muscle spasm after steady temperature increase or decrease (Becker and Genoway, 1979; Beitinger and Bennett, 2000). Some authors suggest muscle spasms should be used for CTM determinations instead of LOE (Bonin et al., 1981; Lutterschmidt and Hutchison, 1997a; Paladino et al., 1980), however in this study both species experienced LOE and muscle spasm nearly simultaneously with no temperature difference between the two endpoints. For each trial, fish from each respective treatment were placed one each into 1 L glass beakers filled with water held at the same start acclimation temperature and suspended in a re-circulating water bath. Oxygen saturation was maintained and thermal stratification prevented by providing moderate aeration to each beaker. Water temperature was increased or decreased 0.3 °C per minute by heating or cooling in a re-circulating bath equipped with a TE-10D Techne Heater or a DS-4 Aqua Logic Delta Star Chiller, and continuously monitored inside the beaker using a Traceable® NIST calibrated thermometer. This rate of temperature change was chosen based on previous studies that showed it is slow enough to track fish body temperature but does not induce thermal acclimation in the fish (Becker and Genoway, 1979; Cox et al., 1974; Lutterschmidt and Hutchison, 1997b). Water temperature was increased or decreased until fish exhibited LOE or muscle spasm (Beitinger and Bennett, 2000; Eme and Bennett, 2009), at which time water temperature was recorded and the fish immediately transferred

to the original acclimation temperature. Gobies were then massed (± 0.01 g), measured (standard length ± 0.1 mm) and returned to their acclimation tank.

2.3. Construction of thermal polygons

The thermal tolerance niche for the two species of gobies was quantified by constructing ecological thermal tolerance polygons (Eme and Bennett, 2009; Fanguie and Bennett, 2003; Taylor et al., 2005). Thermal tolerance polygons were assembled with both thermal tolerance scope (difference between the CTMax and CTMin) and acclimation range, and was expressed quantitatively using area units ($^{\circ}\text{C}^2$). The regression model of CTMax or CTMin on acclimation temperature of fish used in constant-temperature trials was used to define the upper and lower boundaries of the polygon. Division of the polygon was that of thermal tolerance independent of previous thermal acclimation history (i.e., intrinsic tolerance zone) and thermal tolerance gained through acclimation (i.e., acquired tolerance zone) by drawing two horizontal boundary lines across at the lowest CTMax and highest CTMin constant-temperature values (Fanguie and Bennett, 2003).

2.4. Statistical analyses

The effect of the year-long acclimation temperatures on adult size in the two species was analyzed using a two-way analysis of variance (ANOVA) with temperature and species as factors. To test for the effect of adult body size (mass or standard length), acclimation temperature and species on CTmax and CTmin a two-way analysis of covariance (ANCOVA) was run with temperature and species as factors and mass (or standard length) as covariate. If interactions between the factors were found, these are reported following the analyses. Tukey-Kramer multiple comparisons tests (Tukey-Kramer MCT) were used to discriminate between means. Temperature data collected at the sites of fish collection (WWC and Key Largo) were analyzed to determine mean monthly and yearly temperatures, maximum and minimum temperatures, temperature trends (least squares regression). All statistical decisions were based on $\alpha = 0.05$. All statistical analyses were performed in JMP Pro version 11.

3. Results

None of the fishes died during or subsequent to the thermal tolerance trials. Wet mass and standard length in *E. oceanops* were greater than in *E. lobeli* regardless of temperature treatment (2-way ANOVA, $F_{3,94} = 54.85$ $p < 0.0001$) (Table 1). Species, mass or standard length, and acclimation temperature had a significant effect on CTMax and CTMin (2-way ANCOVA, $F_{7,40} = 50.95$, $p < 0.0001$; Figs. 1 and 2; Table 1). Critical thermal maxima (\pm SD) of *E. oceanops* and *E. lobeli* acclimated at temperatures between 20 and 28 $^{\circ}\text{C}$ ranged from 31.8 ± 0.47 $^{\circ}\text{C}$ to 35.5 ± 1.47 $^{\circ}\text{C}$ and 34.9 ± 0.83 $^{\circ}\text{C}$ to 39.1 ± 0.72 $^{\circ}\text{C}$, respectively (Table 1; Fig. 1); CTMax significantly increased at higher acclimation temperatures ($p < 0.0001$), decreased with mass ($p = 0.005$) and standard

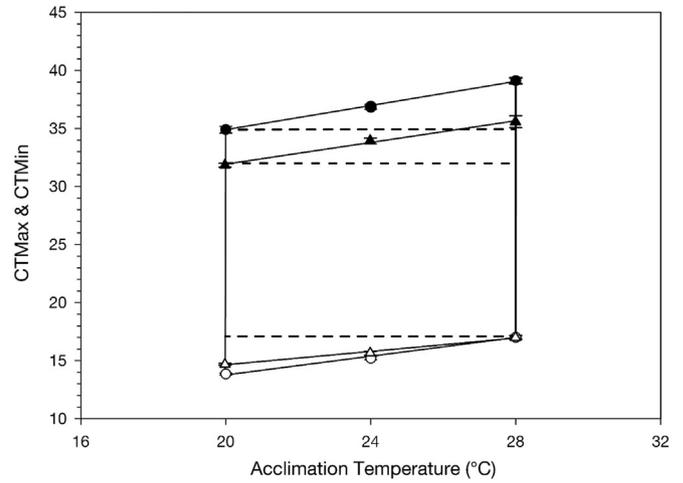


Fig. 1. Ecological thermal polygon with critical thermal minima (CTMin; white symbols) and maxima (CTMax; black symbols) values for *Elacatinus lobeli* (circles) and *E. oceanops* (triangles) acclimated to temperatures between 20 and 28 $^{\circ}\text{C}$. Vertical bars represent 95% confidence intervals. Regression models on acclimation temperature were based on 8 fish each species per acclimation groups ($n = 48$ fish per species). High temperature tolerances are represented by the regression models: $\text{CTMax} = 22.62 + 0.46 \times \text{acclimation temperature}$ ($R^2 = 0.9$, $p < 0.0001$) in *E. oceanops* and $\text{CTMax} = 24.31 + 0.526 \times \text{acclimation temperature}$ ($R^2 = 0.88$, $p < 0.0001$) in *E. lobeli*. Low temperature tolerances are represented by the regression models: $\text{CTMin} = 8.85 + 0.28 \times \text{acclimation temperature}$ ($R^2 = 0.88$, $p < 0.0001$) in *E. oceanops* and $\text{CTMin} = 5.9 + 0.39 \times \text{acclimation temperature}$ ($R^2 = 0.95$, $p < 0.0001$) in *E. lobeli*.

length ($p = 0.02$), and were distinct at each acclimation temperature and between species (Tukey-Kramer MCT, $p < 0.05$). Critical thermal minima (\pm SD) of *E. oceanops* and *E. lobeli* ranged from 14.7 ± 0.25 $^{\circ}\text{C}$ to 17.0 ± 0.54 $^{\circ}\text{C}$ and 13.8 ± 0.24 $^{\circ}\text{C}$ to 17.0 ± 0.24 $^{\circ}\text{C}$, respectively (Table 1; Fig. 1); CTMin were significantly lower at cooler acclimation temperatures ($p < 0.0001$), smaller mass ($p = 0.04$) and distinct at each acclimation temperature (Tukey-Kramer MCT, $p < 0.05$) but not across standard lengths ($p = 0.7$). Low temperature tolerances (CTMin) are represented by the regression models: $\text{CTMin} = 8.85 + 0.28 \times \text{acclimation temperature}$ ($R^2 = 0.88$, $p < 0.0001$) in *E. oceanops* and $\text{CTMin} = 5.9 + 0.39 \times \text{acclimation temperature}$ ($R^2 = 0.95$, $p < 0.0001$) in *E. lobeli* (Fig. 1). High temperature tolerances (CTMax) are represented by the regression models: $\text{CTMax} = 22.62 + 0.46 \times \text{acclimation temperature}$ ($R^2 = 0.9$, $p < 0.0001$) in *E. oceanops* and $\text{CTMax} = 24.31 + 0.526 \times \text{acclimation temperature}$ ($R^2 = 0.88$, $p < 0.0001$) in *E. lobeli* (Fig. 1).

Data from CTM were combined to construct thermal polygons for each species and overlapped to show differences in thermal tolerance (Fig. 1). Total polygon area for *E. oceanops* was 137.6 $^{\circ}\text{C}^2$ and only 18.6% of the tolerance was acquired through acclimation (25.6 $^{\circ}\text{C}^2$). Total polygon area for *E. lobeli* was 172.8 $^{\circ}\text{C}^2$ and only 17.13% was acquired through acclimation (29.6 $^{\circ}\text{C}^2$). Both species are stenotherms, with limited tolerance area. However, *E. lobeli* exhibited higher intrinsic tolerance area (143.2 $^{\circ}\text{C}^2$) when compared to *E. oceanops* (112 $^{\circ}\text{C}^2$).

Table 1

Critical thermal maxima (CTMax), critical thermal minima (CTMin), standard length measurements (SLM), and wet weight mass (WWM) for *Elacatinus oceanops* and *E. lobeli* are grouped by acclimation temperature. The number of fish used in each trial (per acclimation temperature) is indicated below the species name. If significant differences between means (Tukey-Kramer MCT, $\alpha = 0.05$) for CTMax, CTMin, SLM and WWM were found, they are reported as upper case letters (within species) and lower case letters (between species). All experimental values are reported as mean \pm standard deviation ($\bar{x} \pm \text{SD}$).

Acclimation temperature ($^{\circ}\text{C}$)	CTMax $\bar{x} \pm \text{SD}$		CTMin $\bar{x} \pm \text{SD}$		SLM (cm) $\bar{x} \pm \text{SD}$		WWM (g) $\bar{x} \pm \text{SD}$	
	<i>E. oceanops</i> ($n = 8$)	<i>E. lobeli</i> ($n = 8$)	<i>E. oceanops</i> ($n = 8$)	<i>E. lobeli</i> ($n = 8$)	<i>E. oceanops</i> ($n = 16$)	<i>E. lobeli</i> ($n = 16$)	<i>E. oceanops</i> ($n = 16$)	<i>E. lobeli</i> ($n = 16$)
20	$31.8 \pm 0.5^{\text{Aa}}$	$34.9 \pm 0.8^{\text{A}}$	$14.7 \pm 0.2^{\text{A}}$	$13.8 \pm 0.2^{\text{A}}$	$4.40 \pm 0.4^{\text{a}}$	2.79 ± 0.50	$1.48 \pm 0.48^{\text{a}}$	0.38 ± 0.2
24	$33.9 \pm 0.7^{\text{Bb}}$	$36.9 \pm 0.6^{\text{B}}$	$15.7 \pm 0.5^{\text{B}}$	$15.2 \pm 0.3^{\text{B}}$	$4.26 \pm 0.41^{\text{b}}$	2.60 ± 0.24	$2.06 \pm 0.19^{\text{b}}$	0.34 ± 0.06
28	$35.5 \pm 1.5^{\text{Cc}}$	$39.1 \pm 0.7^{\text{C}}$	$17.0 \pm 0.5^{\text{C}}$	$17.0 \pm 0.2^{\text{C}}$	$3.75 \pm 0.58^{\text{c}}$	2.74 ± 0.33	$1.12 \pm 0.64^{\text{c}}$	0.31 ± 0.11
			Overall $\bar{x} \pm \text{SD}$:		$4.13 \pm 0.29^{\text{a}}$	$2.71 \pm 0.14^{\text{b}}$	$1.56 \pm 0.61^{\text{a}}$	$0.35 \pm 0.14^{\text{b}}$

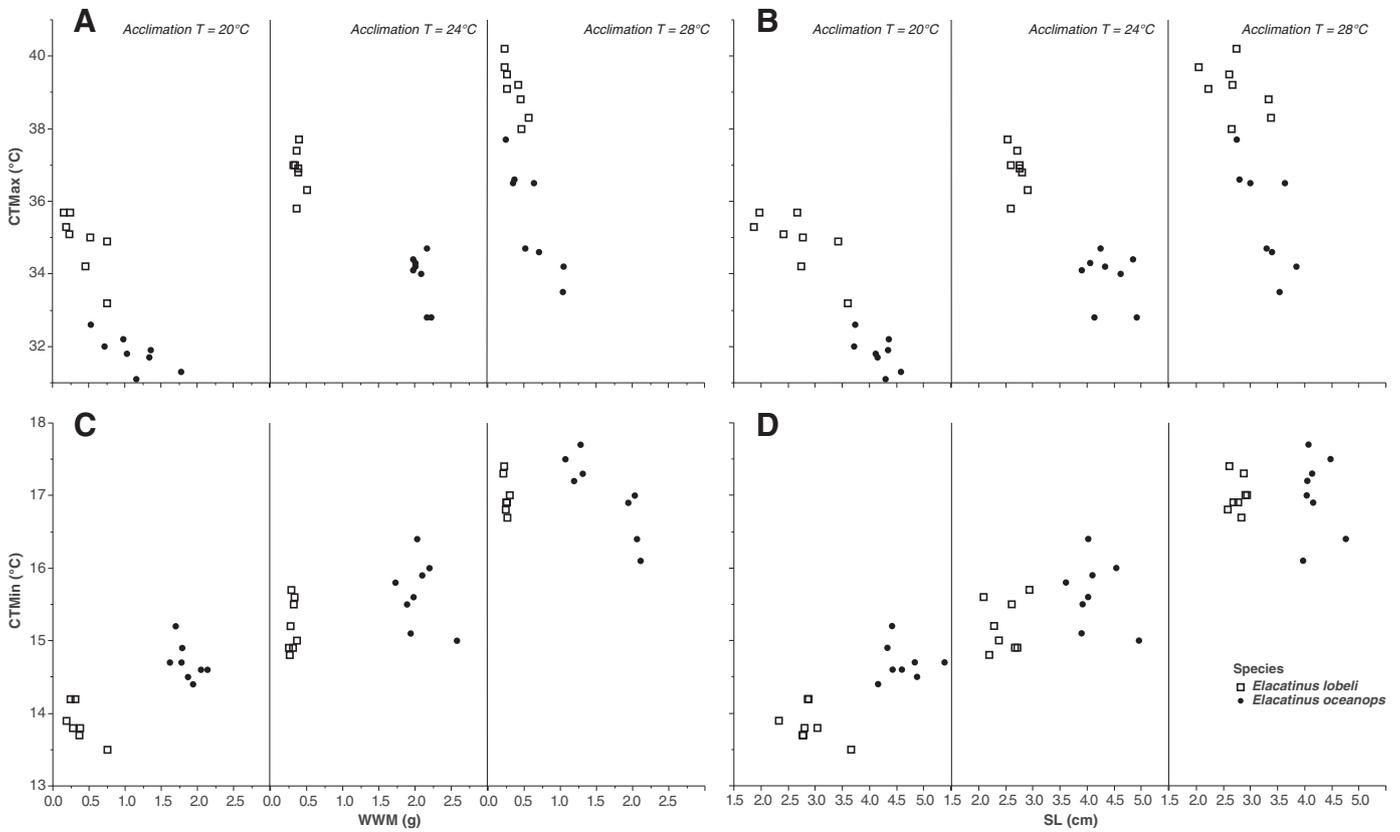


Fig. 2. Wet weight mass (WWM, g), standard length (SL, cm) and critical thermal maxima (CTMax, $n = 24$ per species, $n = 8$ per acclimation temperature) and minima (CTMin, $n = 24$ per species, $n = 8$ per acclimation temperature) in two species of cleaner gobies *Elacatinus lobeli* (square) and *E. oceanops* (closed circle), acclimated at three constant temperatures (T). Each symbol represents an individual fish.

Overall, mean annual, minimum and maximum temperatures at WWC and Key Largo differ (least squares regression, $p < 0.01$). Temperature decreased to 19.7 ± 0.4 °C in Key Largo and 24.6 ± 0.3 °C at WWC ($p < 0.0001$; $R^2 = 0.79$) during the coldest month (January) with an mean T_{min} of 21.6 ± 0.4 °C (Key Largo) and 25.3 ± 0.3 °C (WWC) (mean T_{min} : $p < 0.0001$, $R^2 = 0.70$; Fig. 3). Temperature increased to 31.9 ± 0.1 °C in Key Largo and 30.2 ± 0.1 °C at WWC ($p < 0.0001$; $R^2 = 0.77$) during the warmest month (August) with an mean T_{max} of 31.4 ± 0.2 °C (Key Largo) and 30.0 ± 0.1 °C (WWC) (mean T_{max} : $p < 0.0001$; $R^2 = 0.59$; Fig. 3).

4. Discussion

This study shows an increase in temperature tolerance in smaller cleaner gobies. In fact, the dwarf-size *E. lobeli* had higher CTMax and lower CTmin when compared to *E. oceanops* acclimated at the same constant temperatures. Thermal tolerance was also affected by acclimation temperature. The goby *E. lobeli* exhibited a wider (about 25%) thermal tolerance window than *E. oceanops*, but in both species most of the area was accounted for by intrinsic rather than acquired tolerance, suggesting that both species are stenothermic. The ecological thermal

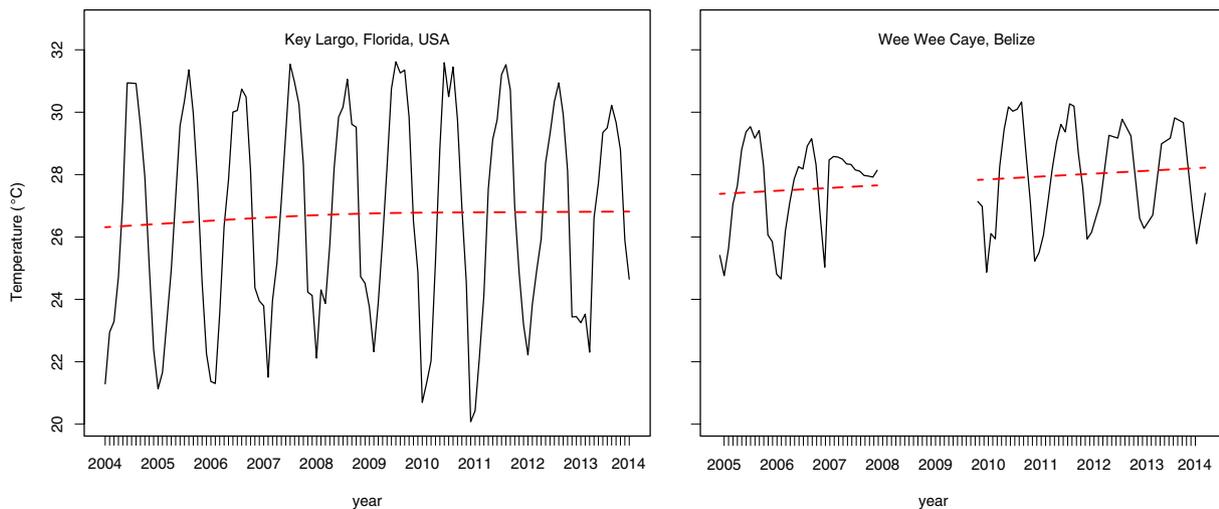


Fig. 3. Monthly average temperatures (continuous line) and temperature trend (dotted line) at Key Largo, USA and Wee Wee Caye, Belize over ten years. Gap in data between 2008 and 2010 from Belize is due to loss of the temperature logger.

polygon area size of these two gobies is comparable to those of extreme stenotherms such as Antarctic icefish of the family Nototheniidae (Somero and DeVries, 1967). When compared to other species of tropical gobies, the species used in this study showed much smaller temperature tolerance areas. The common goby, *Bathygobius fuscus*, and the sandflat goby *Bathygobius* spp., have much wider tolerance areas, 829.1 °C² and 638.8 °C² respectively (Eme and Bennett, 2009). Moreover, the acquired tolerance in these two species were two to three-fold greater than the ones quantified for the cleaner gobies used in this study (Eme and Bennett, 2009).

In the present study a common set of acclimation temperatures was chosen for both species, rather than using individual chronic temperatures, i.e. temperatures at which fishes cease to eat (Currie et al., 1998), for two reasons: 1) chronic stress is known to affect body size (Gillooly et al., 2001) and 2) we wanted to use the same temperature treatments across species in a common garden experimental design. Therefore, the acclimation temperatures were chosen to ensure fish survival from juvenile to adult stage (~one year) in both species. It is possible that absolute thermal tolerance scope might have been slightly underestimated due to the experimental design and that gobies at different life stages may be able to acclimate to slightly higher or lower temperatures than juveniles and therefore increase their overall thermal tolerance. In this study however, the goal was to analyze the role of size on CTM and therefore the approach was to opt for a fixed, common set of long-term acclimation temperatures.

Smaller cleaner gobies exhibited higher thermal tolerance. As extreme seasonal temperatures are predicted to increase in frequency and magnitude with current climate change (Seneviratne et al., 2014), organisms have a higher chance of experiencing acute thermal stress. Larger fishes could exploit thermal patchiness in the environment during extreme events by selecting preferred temperatures in deeper water refugia (Di Santo and Bennett, 2011a), albeit this hypothesis needs to be confirmed with field and laboratory studies. Furthermore, mass and acclimation temperature affected also low thermal tolerance significantly. The tendency to find larger aquatic ectotherms in colder environments has been widely documented in a number of vertebrates and invertebrates (Atkinson, 1994; Gillooly et al., 2001) and this response of body size to environmental temperature may be plastic or adaptive (Atkinson and Sibly, 1994). Although most studies focused on plastic responses of body size, there is some evidence that genetically larger individuals can be selected at low temperatures and some species show a latitudinal gradient in body size that correlates negatively with temperature (Atkinson and Sibly, 1994; Di Santo, 2015; Partridge et al., 1994). In fact, large individuals may increase growth efficiency by reducing expensive respiratory surfaces at low temperatures. In this case, however, smaller fishes tended to be more tolerant to both lower and higher temperatures. Here are presented three possible hypotheses that may explain higher thermal tolerance in smaller gobies.

First, the slightly different environment experienced by these gobies on a daily and annual basis could explain the difference in tolerance. Daily thermal fluctuations in the environment have been found to increase thermal limits in ectotherms (Kern et al., 2015). However, the present data do not seem to explain fully this general pattern. In fact, although average and mean maximum temperatures across the past decade were significantly higher at WWC when compared to Key Largo (~1 °C), *E. oceanops* at Key Largo experience significantly higher temperature peaks (T_{max}) during the hottest month of the year (~1.5 °C) than *E. lobeli*, and it would then be expected to observe higher thermal tolerance in the larger goby species that lives in more fluctuating environments (Chen et al., 2015). Therefore, in this system, mass and/or average temperature rather than T_{max} experienced in nature could justify the differences in thermal tolerance observed.

Second, differences in intraspecific thermal tolerances suggest that similar-age but smaller individuals are better able to cope with rapidly changing temperatures. Increased tolerance in smaller ectotherms may be associated with behavioral and ecological phenomena, such as

dominance and subordination observed in social hierarchies, as seen in cleaner gobies (Whiteman and Côté, 2004), rather than a physiological effect of body mass per se. In fact, dominant and larger fishes are known to displace and limit subordinate and smaller individuals to marginal, low quality environments (Magnuson et al., 1979). Work by Bennett and co-authors has documented that smaller and juvenile fishes spend a prolonged period of time (sometimes years) in shallow nursery areas and are likely to experience wider thermal fluctuations than larger individuals (DiGirolamo et al., 2012; Di Santo and Bennett, 2011a, 2011b; Fangue and Bennett, 2003; Wallman and Bennett, 2006). In freshwater post-glacial lakes, normal-size and dwarf salmonid fishes of the genus *Coregonus* are also known to partition resources according to temperature by segregating by depth and have modified digestive and growth processes to exploit their thermal niche (Ohlberger et al., 2008). The link between social interactions and habitat preferences should be further investigated to elucidate any role in thermal tolerance (Wong, 2012).

Third, it has been suggested that thermal tolerance may be dictated by the capacity to deliver oxygen to tissues in fishes. The Oxygen-Capacity-Limited-Thermal-Tolerance (OCLTT) hypothesis suggests that oxygen availability limits both thermal tolerance and the maximum body size in ectotherms (Pörtner, 2010; Pörtner and Knust, 2007). As temperature increases, metabolic rates and gill ventilation of fishes accelerate while dissolved oxygen decreases, thus creating a mismatch between oxygen demand and supply to the tissues (Pörtner and Farrell, 2008). The physiological limitation to higher thermal tolerance may be represented by the gill surface area (Freedman and Noakes, 2002; Pauly, 2010). Even if fishes may increase gill filaments volume with body size, gas-exchange occurs in the first mm length of the gill capillaries and therefore larger filaments would not directly enhance oxygen uptake (Freedman and Noakes, 2002). Furthermore, remodeling of respiratory surfaces and higher ventilation rates are metabolically expensive (Forster et al., 2012; Pauly, 2010; Verberk et al., 2011). Upper thermal limits and survival of eelpout (*Zoarces viviparus*) in the field are inversely correlated with size (Pörtner, 2010). In addition, smaller fishes exhibit lower critical dissolved oxygen levels than larger fishes (Cech et al., 1979), thus suggesting that small body size may confer a physiological advantage during acute temperature-related oxygen challenges (Burlinson et al., 2001). Indeed, hypoxia is known to reduce upper thermal tolerance in mudskipper, *Periophthalmus kalolo*, by 2 °C and in *G. fuscus* by 0.5 °C (Taylor et al., 2005). These results align with the hypothesis that the Lilliput effect could be produced by dwarfing or the differential survival of smaller individuals as a response to environmental change (Harries and Knorr, 2009), in particular warming and shallow marginal settings (Keller and Abramovich, 2009). During several past climatic shifts, biodiversity declined and many large organisms went extinct, resulting in the dominance of hypoxia- and temperature-tolerant smaller individuals (Keller and Abramovich, 2009; Sun et al., 2012). Although the validity of the OCLTT has been debated (Clark et al., 2013; Jutfelt et al., 2014; Pörtner, 2014), it may help explain at least the upper temperature tolerance in smaller fishes. Further studies are however necessary to elucidate the mechanisms underlying wider thermal windows in smaller cleaner gobies.

5. Conclusions

Results from this study suggest that smaller cleaner gobies tend to be more tolerant to acute changes in temperature when compared to larger conspecifics and congeners, but comparisons with multiple species are needed to extend the observed pattern to other cleaner gobies (for taxonomic review of Caribbean *Elacatinus* spp., see Randall and Lobel, 2009) and more groups of fishes. A shift towards smaller body size could have a significant effect on interactions within marine communities by reducing overall fish biomass (Perry et al., 2005). Although identifying responses to temperature challenges is useful in single species, it is difficult to predict shifts in multi-species interactions based solely on

isolated or few thermal sensitivity tests. Nonetheless, as body size seems to be at least implicated in both thermal tolerance and sensitivity of cleaner gobies (Di Santo and Lobel, 2016), future studies could benefit from testing a wide range of different sized adult individuals rather than a narrow one, if the goal is to forecast more realistic responses of species to warming (Di Santo, 2016).

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