

Thermal tolerance and metabolic responses of two damselfish species from a hyperthermic rockpool nursery in Dry Tortugas National Park, USA

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ABSTRACT- Beachrock formations on Loggerhead Key in Dry Tortugas National Park, USA are an important nursery for many juvenile reef fishes. Wide variations in temperature are common in these areas and can markedly influence fish metabolism and thermal tolerance. We determined routine resting metabolic rate and temperature quotient (Q_{10}) at 24 and 32°C. Thermal tolerance (measured as critical thermal maximum, CT_{max}) was also measured for sergeant major (*Abudefduf saxatilis*) and cocoa damselfish (*Stegastes variabilis*) acclimatized to beachrock nursery temperatures. Sergeant majors occupied shallow rockpool margins that experience rapid, extreme temperature changes. These fish exhibited relatively low metabolic rates, reduced Q_{10} values (2.40), and relatively high levels of temperature tolerance (CT_{max} = 40.0°C). Cocoa damselfish selected deeper, more thermally stable rockpool areas. These fish had higher metabolic rates, were more sensitive to temperature increase (Q_{10} = 2.84), and were less tolerant of high temperatures (CT_{max} = 38.6°C) than sergeant majors. Metabolic and temperature tolerance adaptations of juvenile sergeant majors and cocoa damselfish allow these fishes to exploit a variety of microhabitats found in beachrock areas on Loggerhead Key.

KEYWORDS. — Cocoa damselfish, Loggerhead Key, Q_{10} , sergeant major, tidepool

INTRODUCTION

Intertidal beachrock formations are produced by near-shore lithification and erosion processes that result in shallow, structurally complex formations. Where they occur at beach margins, beachrock zones are ideally suited as nursery grounds for juvenile fishes, many of which later recruit to nearby reefs. Although common to the Bahamas and Bermuda (Purdy 1963), beachrock nursery habitats are rare in the United States, with the Loggerhead Key formation (24°38.08'N 82°55.24'W), in Dry Tortugas National Park (DTNP) being the best studied (Ginsburg 1953; Shinn 2009).

The Loggerhead Key formation is a thriving nursery area that helps support DTNP fish biodiversity and reef health. Longley and Hildebrand (1941), for example, reported that as many as 10% of Tortugas fish species utilize the formation as a nursery, and Lindeman et al., (2000) designated the area as essential nursery habitat. Several damselfish species are known to utilize the Loggerhead Key nursery (Rummer et

al. 2009) including, cocoa damselfish (*Stegastes variabilis*), night sergeants (*Abudefduf taurus*), sergeant majors (*Abudefduf saxatilis*), and beaugregory (*Stegastes leucostictus*). Damselfishes are considered to be a keystone group in coral reef habitats (Hixon and Brostoff 1983), and one that plays an important role in shaping the structure, fauna and ecology of patch reefs in DTNP (Wallman et al. 2004; Wilkes et al. 2008).

At low tide, Loggerhead Key beachrock areas are reduced to a series of shallow rockpools that experience rapid shifts in temperature. Rummer et al., (2009) reported that temperatures in these pools during June 2001 ranged from 25.9 to 33.2 °C, and Fanguie et al., (2001) measured temperatures of nearly 36°C during a June, 2000 rockpool study. Even higher temperatures are likely during the later summer months, for example, Pearse (1934) measured August water temperatures of 42.9 °C in brackish pools on nearby Long and Garden Keys in DTNP. Little is known about how juvenile damselfishes cope

with rising rockpool temperatures. Fanguie et al., (2001) and Rummer et al., (2009) report respective upper thermal tolerance values of 36.1 and 37.6°C for cocoa damselfish; values that closely approached temperatures measured in their nursery environment. It was suggested that this species avoided the most extreme pool temperatures by exploiting deeper, cooler water (Fanguie et al. 2001). The same may be true of beaugregory and night sergeant damsels which are not present in shallow rockpools at low tide (Rummer et al. 2009). Sergeant majors, on the other hand, frequent shallow, exposed pool areas where temperatures become most extreme (Rummer et al. 2009; personal observation). In addition to its role as a directing factor, rising water temperatures also act as a controlling factor by altering metabolic demand (Fry 1946). In cases where temperature increases are extreme, fish may find metabolic thermal sensitivity to be a greater threat to survival than potentially lethal high temperatures (Brown 1989; Eme and Bennett 2009).

The purpose of our study was to evaluate metabolic and temperature tolerance responses of juvenile sergeant major and cocoa damselfish inhabiting rockpools of Loggerhead Key, DTNP. Our specific objectives were to 1) measure routine resting metabolic rates and use these values to determine temperature quotients (Q_{10}) across the temperature range commonly encountered in Loggerhead Key rockpool habitats, and 2) to compare heat tolerance (i.e., critical thermal maximum) of both species acclimatized to rockpool conditions. Evaluating the impacts of diel temperature change on damselfish thermal tolerance and bioenergetic responses will provide a greater understanding of how temperature may influence juvenile damselfish distribution in nursery habitats.

MATERIALS AND METHODS

Collection and Holding Conditions

Metabolic and temperature tolerance studies were conducted from 4 May to 6 May 2010 and all values reported as mean \pm standard deviation. Damselfishes were netted

from beachrock habitats on Loggerhead Key, DTNP during daytime low tide at temperatures between 26.8 and 31.5°C. Fish were transported to the *R/V Bellows* in holding tanks filled with clean seawater circulated by a battery operated aerator. All sergeant majors were determined to be young-of-the-year juveniles, while cocoa damselfish were staged as late juveniles based on color phase and size (Smith 2002). Prior to experimental trials, fish were held for 24 h at 25°C in replicate flasks supplied with flow-through sea water. Handling stress was minimized by keeping fish in the same replicate flask during the holding period as well as during the metabolic or temperature tolerance trials. During metabolic trials, cocoa damselfish were placed individually into 500 ml flasks (12 replicates), but because of their small size (mean 0.21 g) and schooling nature, sergeant majors were kept together in 250 ml flasks in groups of five (3 replicates) or six (11 replicates) fish per flask. Both species were individually housed for temperature tolerance experiments. Upon completion of experiments, fish were released at their site of capture.

Flow-through Respirometry

Flow through respirometry (Cech 1990) was used to estimate routine resting oxygen consumption rates ($\text{mgO}_2 \text{ h g}^{-1}$) for 12 cocoa damselfish and 14 groups of sergeant majors at 24 (± 0.1) and 32 (± 0.1) °C. For each trial, a flask containing either sergeant majors, or a single cocoa damselfish was placed into a temperature controlled, 75-L reservoir filled with filtered (30 μ plankton net) seawater. A control flask was run during each trial to account for non-fish respiration. Seawater was pumped from the reservoir (Model 258 GPH submersible fountain pump) to an aerated headbox and flowed via gravity into the respirometry and control flasks, both of which emptied back into the reservoir. Respirometer flow rates were adjusted using polypropylene stopcocks (1 cm O.D.) so as to produce an oxygen concentration difference of 10-15% between inflow and outflow water (Steffensen 1989; Cech 1990). Data collection

began after the inflow-outflow oxygen content reached 99% equilibrium as determined from the flow rate and volume of each flask (Steffensen 1989; Cech 1990). Inflow and outflow water samples were simultaneously collected at 30 minute intervals ($n = 4$) in 300-ml Biological Oxygen Demand (BOD) bottles, and dissolved oxygen values ($\pm 0.005 \text{ mg L}^{-1}$) determined using standard Winkler titration methods (Cox 1990). Metabolic rate of fish from each flask was determined from the standard equation:

$$\dot{M}_{O_2} = (C_{O_2(i)} - C_{O_2(o)}) \dot{V}_w$$

where, \dot{M}_{O_2} is routine resting oxygen consumption rate ($\text{mgO}_2 \text{ h}^{-1}$), $C_{O_2(i)}$ is oxygen concentration of inflow water ($\text{mgO}_2 \text{ L}^{-1}$), $C_{O_2(o)}$ is oxygen concentration of outflow water ($\text{mgO}_2 \text{ L}^{-1}$), and \dot{V}_w is the water flow rate through the respirometer (L min^{-1}). Routine resting metabolic rate for each species at each temperature was taken as the mean of the replicate values. To avoid directional confounding effects, metabolic rates of one-half of fish from each species were determined first at 24°C and again following an acute temperature increase to 32°C over a 30 minute interval. Remaining fish were subjected to the reciprocal temperature protocol. Data for each species were pooled for all measures at 24°C and all measures at 32°C regardless of the sequence of temperature exposure. Temperature quotients (Q_{10}) were estimated for each species using the equation (Schmidt-Nielsen 1997):

$$Q_{10} = (K_2 \div K_1) \frac{10}{T_2 - T_1}$$

where, Q_{10} is the temperature quotient and K_2 and K_1 are mean metabolic rates at temperatures T_2 (32°C) and T_1 (24°C), respectively. Following trials, wet mass ($\pm 0.01 \text{ g}$) and standard length ($\pm 0.01 \text{ cm}$) were determined for all fish.

Mean mass of sergeant majors and cocoa damselfish were compared using Student's t-test ($\alpha = 0.05$). Metabolic rate values for high and low temperature treatment groups were compared

within species using Paired t-test analysis with the Bonferroni correction ($\alpha = 0.025$). Between species metabolic rate comparisons were made using repeated measures ANCOVA on log-transformed data with mass as a covariate (Packard and Boardman 1987; 1999).

Determination of Critical Thermal Maxima

Standard Critical Thermal Methodology (Cox 1974; Becker and Genoway 1979; Beitinger et al. 2000) was used to estimate heat tolerance as critical thermal maxima (CTmax) for 16 sergeant majors and 14 cocoa damselfish. Briefly, fish were placed one each into a 500-ml Erlenmeyer flask and submerged into a 50 L re-circulating water bath at 26°C . Temperatures were then increased at $0.30^\circ\text{C min}^{-1}$, 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 one minute (Beitinger et al. 2000). After LOE was reached, fish wet mass ($\pm 0.01 \text{ g}$) and standard length ($\pm 0.01 \text{ cm}$) was measured, and fish returned to 26°C seawater to recover. Critical thermal maximum was calculated as the mean of the LOE temperatures for each species, and values compared using Student's t-test ($\alpha = 0.05$).

RESULTS

During this study, Loggerhead Key rockpools experienced marked diel temperature shifts as well as discrete patterns of thermal stratification. Rockpool temperatures ranged between approximately 24 and 32°C from early morning to mid-afternoon (average midday temperature = 28.4°C) depending on tidal stage. The most rapid temperature increases were seen at low tide between the hours of 10:00 and 14:00 when rockpool temperatures climbed from around 27 to 32°C at a rate of $1.2^\circ\text{C per hour}$. Temperatures in deeper rockpool areas (mean = 0.91 m) were on average 2.3°C cooler than

shallow pool margins (mean = 0.30 m). At low tide, cocoa damselfish remained in deeper pool zones close to beachrock ledges or outcroppings, whereas sergeant majors were most abundant at pool margins, sometimes in depths as shallow as 6 to 8 cm or less.

Damselfishes in our study exhibited notably different metabolic responses to temperature (Table 1). Routine resting oxygen consumption rates for sergeant major at 24 and 32°C were lower (0.128 and 0.250 mg h⁻¹ g⁻¹) than those of cocoa damselfishes (1.645 and 3.685 mg h⁻¹ g⁻¹). In addition, intraspecific metabolic rates were significantly lower at 24°C than at 32°C for sergeant majors (Paired t-test, $t_{13} = -5.61$, $P < 0.0001$), as well as cocoa damselfish (Paired t-test, $t_{11} = -2.87$, $P = 0.0151$). Significant differences in body mass (Table 1) were also found between the two species (Student's Independent t-test, $t_{24} = 7.60$, $P < 0.00001$). Even after controlling for fish mass, differences between metabolic rates measured at both treatment temperatures were significantly lower for sergeant majors than cocoa damselfish (Repeated measures ANCOVA, $F_{2,23} = 4.45$, $P = 0.0450$). Adjusted least square mean values of oxygen consumption at low and high temperature was 0.143 and 0.272 mg h⁻¹ g⁻¹ for sergeant majors, and 1.066 and 2.411 mg h⁻¹ g⁻¹ for cocoa damselfish.

Sergeant majors were less sensitive to changing temperatures, but more tolerant of high temperatures than cocoa damselfish (Table

1). Temperature quotients calculated from routine resting metabolic rates were 2.40 for sergeant majors and 2.84 for cocoa damselfish. In addition, the respective critical thermal maxima for field acclimatized sergeant major (40.0°C) and cocoa damselfishes (38.6°C), were statistically distinct (Student's t-test, $t_{28} = 2.37$, $P = 0.0249$).

DISCUSSION

Microhabitat selection is the major factor determining the thermal acclimatization state of sergeant major and cocoa damselfishes within the Loggerhead Key rockpool nursery. Because of their small size (ca. 2 cm), sergeant majors can effectively exploit shallow rockpool margins that are inaccessible to larger competitors and predators. Mid-day water temperatures in these shallow refugia are high, especially so during low tide, and would account for the fishes' relatively high thermal tolerance level. In contrast, the much larger cocoa damsels establish algal gardens in cooler, deeper rockpool zones, and not unexpectedly, exhibited thermal tolerance values lower than those measured in sergeant majors. Regardless of their previous thermal history, tolerance values of both damselfishes exceeded the highest pool temperatures we measured in early May. During later summer months, however, shallow water areas in DTNP experience much higher temperature peaks (Pearse 1934) that no doubt

TABLE 1. Summary of size, metabolic rate (at 24 and 32°C), temperature quotient (Q_{10}) and high thermal tolerance (CTmax) of sergeant major, *Abudefduf saxatilis*, and cocoa damselfish, *Stegastes variabilis*, from a hyperthermic beachrock nursery in Dry Tortugas National Park, USA.

Mass (g)	Standard		$\dot{M}O_2$ at 24°C (mg h ⁻¹)	$\dot{M}O_2$ at 32°C (mg h ⁻¹)	Q_{10}	CTmax (°C)
	Length (cm)					
Mean ±SD	Mean ±SD		Mean ±SD	Mean ±SD		
Sergeant Major, <i>Abudefduf saxatilis</i>						
0.207 ±0.001	16.0 ±4.60		0.128 ±0.016	0.250 ±0.025	2.40	40.0 ±0.41
Cocoa Damselfish, <i>Stegastes variabilis</i>						
3.250 ±0.433	47.8 ±10.76		1.645 ±0.282	3.685 ±0.700	2.84	38.6 ±0.36

affect fish temperature responses. Sergeant majors are capable of surviving temperatures over 40°C by early spring, and while no other thermal tolerance data are available for this species, it seems likely that tolerance levels will increase further as temperatures rise in the shallow rockpool margins. Cocoa damselfish on the other hand, are more likely to use behavioral adaptations to avoid problems associated with high temperatures (Fangue et al. 2001). By selecting deeper pool areas cocoa damselfish experience peak temperatures nearly 2.5°C lower than those occurring at the rockpool margins. Critical thermal maximum determinations for field acclimatized cocoa damselfish by Fangue et al., (2001), Rummer et al., (2009), and the present study suggest a thermal acclimation scope for the species between 36 and 39°C; a range that would provide adequate protection against increasing summer temperatures with little further modification of upper thermal tolerance limits.

With few exceptions, larger fish exhibit higher overall rates of metabolism than smaller fish all other factors being equal, but when reconciled for mass the relationship is reversed (Schmidt-Nielsen 1997). Mass-specific routine resting metabolic rates for the more massive cocoa damselfish were an order of magnitude higher than rates measured for sergeant majors, but a more unusual finding was that this relationship persisted even after values were statistically adjusted for mass. This finding may be related to differences in temperature compensation response which are independent of body mass (Newell and Northcroft 1967; Feder and Hofmann 1999). Other closely related marine species show varying levels of compensation when faced with increasing water temperatures, in which one species exhibits markedly higher metabolic rates than the other following a change in environmental temperature (Targett 1978; Vettera 1982). For sergeant majors, muted metabolic responses allow the fish to limit costs associated with the exponential metabolic increases that accompany changing environmental temperatures. In addition, while most ectotherms demonstrate a doubling of

metabolic rate with every 10°C rise in ambient temperature (Schmidt-Nielsen 1997), some tide pool fishes can limit metabolic rate increases by altering biochemical pathways to operate across a wide temperature range (Somero and Devries 1967; Brown 1989; Eme and Bennett 2009). Both damselfish exhibited Q_{10} values greater than 2. Even so, sergeant majors were markedly less sensitive to temperature increases than cocoa damselfish, a response better suited to the capricious thermal conditions experienced in very shallow water habitats.

Beachrock areas on Loggerhead Key are especially well suited as nursery areas for juvenile damselfishes. The habitats are all but inaccessible to large predators and the complex architecture of overlapping beachrock provides a variety of microhabitats which can be exploited by juvenile fishes that have adaptations to survive harsh thermal conditions. Temperature acts as a directing factor in the rockpool environment shaping distribution patterns and reducing direct space competition between syntopic fishes. Cocoa damselfish prefer the more complex beachrock cover present in deeper pools. Lower ambient temperatures in these areas allow the fish to survive with lower levels of thermal tolerance and avoid adverse effects resulting from relatively high levels of temperature sensitivity. Sergeant majors are physiologically well-adapted to endure thermal conditions in the very shallow rockpool environment by virtue of their high thermal tolerance, inherently low metabolic rates, and reduced temperature sensitivity.

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