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PRIMARY RESEARCH PAPER

Juvenile Ribbontail Stingray, *Taeniura lymma* (Forsskål, 1775) (Chondrichthyes, Dasyatidae), demonstrate a unique suite of physiological adaptations to survive hyperthermic nursery conditions

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Abstract Juvenile ribbontail stingrays, *Taeniura lymma* (Forsskål, 1775) of the tropical West Pacific inhabit mangal and seagrass nurseries that often experience rapid and extreme increases in water temperature. We hypothesized that juvenile rays possess a thermal strategy similar to other hyperthermic specialists, in which fish prefer high temperatures, are always prepared for thermal extremes regardless of previous thermal history, and exhibit low metabolic thermal sensitivity. Critical thermal methodology was used to determine the thermal niche, and a thermal gradient used to estimate stingray final preferendum. Temperature quotients (Q_{10}) were calculated from metabolic rates determined at three temperatures using flow-through respirometry. As predicted, juvenile rays showed a relatively small thermal niche dominated by intrinsic tolerance with limited capacity for acclimation. Thermal preference values were higher than those reported for other elasmobranch species. Interestingly, the temperature quotient for juvenile rays was higher than expected, suggesting that these fish may have the ability to exploit the thermal heterogeneity in their environment. Temperature likely acts as a directing factor in this species, separating warm tolerant juveniles from adults living in deeper, cooler waters.

Keywords Temperature preference · Q_{10} · Metabolism · Temperature tolerance polygon · CTM · Elasmobranch

Introduction

Fishes living in challenging thermal habitats typically use an array of tactics to mitigate the consequences of exposure to potentially dangerous temperatures (Fangue & Bennett, 2003; Taylor et al., 2005). Ameliorative responses can be organized into three non-mutually exclusive categories (see Beitinger & McCauley, 1990). Behavioral reactions are a first line of defense against environmental perturbations, and are characterized by preference/avoidance responses (Coutant, 1977; Beitinger & McCauley, 1990; Wallman & Bennett, 2006). Behavioral reactions can be mobilized in seconds to minutes and are perhaps the most important but least appreciated category of adaptive response. Physiological responses are the second defense against harsh temperatures, and are exemplified by a readjustment in tolerance endpoints,

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typically occurring over a course of hours to weeks (Reber & Bennett, 2007; Schulte et al., 2011). The final and most extensive response to changing thermal conditions involves biochemical alterations of metabolic pathways or synthesis of new molecules (e.g., allozymes or isozymes); changes that often take days or weeks to accommodate (Hochachka & Somero, 1973, 2002; Angilletta et al., 2006; Schulte et al., 2011).

Behavioral, physiological, and metabolic data can reveal key components of a fishes' overall thermal tolerance strategy. For example, fishes placed in a thermal gradient will select a discrete temperature preferendum (Coutant, 1977), a value widely interpreted as the temperature at which many physiological functions are optimized. Preferenda play a key role in dictating fish distribution, growth and activity patterns (Coutant, 1977; McCauley & Huggins, 1979). Likewise, heat and cold tolerance values measured across a range of acclimation temperatures can be used to define a polygonal area that delineates a species' fundamental thermal niche (Beitinger et al., 2000). The polygon position, size, and shape identify specific tactics used to cope with prevailing thermal conditions (Eme & Bennett, 2009b), and the relationship between acclimation temperature and thermal tolerance provides insight into temperature acclimation patterns (Claussen, 1977). Metabolic responses to acute temperature change are indicators of biochemical pathway features that are linked to animal bioenergetics. Responses to acute temperature shifts are used to quantify metabolic sensitivity and are often expressed as a temperature quotient or Q_{10} value. Ectotherm metabolic rates typically double (i.e., $Q_{10} = 2$) with each 10°C increase in ambient temperature (Schmidt-Nielsen, 1997), but deviations from the norm may improve energy budgets of fishes living in heterogeneous thermal environments (Hopkins & Cech, 1994; Eme & Bennett, 2009a; Di Santo & Bennett, 2011). Empirical physiological evidence is the basis for understanding fish thermal ecology and often has practical uses in predicting how fish may respond to changing habitat conditions.

While a large number of empirical studies evaluate one or more adaptive thermal responses in bony fish, elasmobranch fishes are not as well represented in the thermal ecology literature. Often thermal relationships of shark or ray species are inferred from movement patterns and distributions of these fishes in nature. For example, dogfish, *Scyliorhinus canicula* (Linnaeus, 1758), and lemon shark, *Negaprion brevirostris* (Poey, 1868), are thought to exploit environmental thermal heterogeneity to improve feeding and digestion, whereas the round stingray, *Urobatis halleri* (Cooper, 1863), may seasonally aggregate in warmer waters for the purposes of reproduction (Sims et al., 2006; DiGirolamo et al., 2012; Vaudo & Lowe, 2006, respectively). Most elasmobranch work in the laboratory has focused on the effects of temperature change on metabolism (e.g., Hopkins & Cech, 1994; Matern et al., 2000; Di Santo & Bennett, 2011). In contrast, thermal preferenda are known for only three elasmobranch species. Casterlin & Reynolds (1979) monitored diel preferenda of the smooth dogfish, *Mustelus canis* (Mitchill, 1815), Crawshaw & Hammel (1973) looked at brain stem temperature and thermotaxis in the horn shark, *Heterodontus franscisi* (Girard, 1855), and Wallman & Bennett (2006) evaluated Atlantic stingray, *Dasyatis sabina* (Lesueur, 1824), preferenda relative to parturition and feeding. Tolerance responses to temperature change have received even less attention with complete heat and cold tolerance profiles known only for the Atlantic stingray (Fangue & Bennett, 2003).

This study identifies behavioral, physiological and metabolic thermal adaptations of juvenile ribbontail stingrays, *Taeniura lymma* (Forsskål, 1775), by quantifying temperature preference, thermal acclimation responses, and metabolic temperature quotients. In combination, these endpoints provide a comprehensive description of the stingrays' thermal ecology when interpreted relative to habitat thermal conditions. Our data clarify relationships between environment, physiology, and behavior in a group that is rarely the focus of such studies, but nonetheless one of great importance to the health and biodiversity of tropical reef systems.

The ribbontail stingray is common to coral reefs and reef-associated habitats throughout the Indo-West Pacific (Last & Stevens, 1994; Nguyen & Nguyen, 2006). A desirable fishery species in many areas (Fowler et al., 1997; Teh et al., 2005; White & Dharmadi, 2007), the rays are commonly taken by intensive fisheries operations near shallow coral reefs (Cavanagh et al., 2003; IUCN, 2011). Ribbontail rays are also the apex predator in benthic habitats across their range (Vonk et al., 2008), feeding on soft-bodied annelids, small bivalves, crustaceans (Last & Stevens, 1994; Michael, 1993), and cephalopods (Huffard, 2007) they expose by excavating deep pits in sandy zones (El-dawi, 2000; Meysman et al., 2006, Garrone-Neto & Sazima, 2009). Consequently, these fish play an important ecological role as bioturbators, shaping benthic morphology as well as determining density and distribution patterns of benthic infauna (Bennett, 2010; O'Shea et al., 2011). Interestingly, adult and juvenile fish occupy dissimilar habitats. Adult rays are found in cool deeper reef environments (Chin et al., 2010) at temperatures between ~22 and 24°C, whereas juveniles frequent warm, shallow intertidal seagrass, mangal, or rocky shoreline habitats (Lugendo et al., 2007; Bennett, 2010; O'Shea et al., 2011) where temperatures generally range between 24 and 32°C (Eme & Bennett, 2009a). By providing foraging areas that are inaccessible to larger predatory fishes such as sharks and groupers, intertidal zones function as nurseries for the juvenile fish before they recruit to the reef (Bennett, 2010). Shallow nurseries, however, are prone to rapid, large-scale temperature increases (Taylor et al., 2005, Eme & Bennett, 2009a). Recently, concerns have been raised about the effect of increasing water temperatures on shallow water elasmobranchs, and juvenile ribbontail stingray populations may be especially vulnerable (Chin et al., 2010). The decline of ribbontail stingrays from over-fishing and changing habitat conditions in many areas of the Indo-West Pacific has prompted the International Union for Conservation of Nature and Natural Resources to classify the species as near-threatened (IUCN, 2011). Given the ecological and economic importance of ribbontail stingrays, as well as their declining numbers, a better understanding of this species could be useful in developing effective management strategies for these fish and their nursery habitats.

Materials and methods

Collection and holding conditions

Ribbontail stingrays ($n = 66$) were collected from a shallow mangal nursery off Hoga Island, southeast Sulawesi, Indonesia (05°27.53′S, 123°46.33′E). Fish had disk widths between 10.2 and 19.8 cm and masses between 85.0 and 390.0 g. White & Dharmadi (2007) reported that males do not become sexually mature until reaching a disk width of 21 cm, and it was assumed all study fish were juveniles. Collections were made with hand-held landing nets or 10-m monofilament seines (3 × 3 cm mesh). Captured rays were transported to the Hoga Island Research Laboratory in aerated 40-l insulated buckets (radius = 42 cm; height = 90 cm) and transferred into 2,000-l holding tanks containing seawater at 27.0 ± 0.3°C and 33 ± 2‰. All temperatures were measured using a calibrated mercury thermometer (National Institute of Standards and Technology). Water quality was maintained by biological filtration augmented with daily seawater exchanges. Stingrays were held under natural lighting conditions (12:12 h L:D diel photoperiod) and fed fresh chopped tuna ad libitum every other day. Fish were placed into experimental trials only after they began actively feeding. Individual ribbontail rays were used in only one experiment (i.e., no fish were reused in trials), and upon completion of experiments all fish were released at their site of capture.

Temperature preference

Ribbontail stingray temperature preference was determined following published standard procedures (Coutant, 1977; Reynolds & Casterlin, 1979; Wallman & Bennett, 2006). Fish were exposed to a thermal gradient of 24–32°C, a range closely approximating intertidal temperatures occurring in their nursery habitat (Eme & Bennett, 2009a). The temperature preference apparatus consisted of an aluminum chamber (3.20 × 0.20 × 0.20 m) positioned 50 cm above a linear bank of ten, 250 W heat lamps that could be turned on or off depending on need. The apparatus contained 65 L of seawater when in use. The temperature gradient was established by running 14°C seawater from a chilled reservoir into one end of the chamber at a rate of 6 l/h; a rate that promoted mixing and prevented vertical temperature stratification. As water flowed along the chamber length, it was progressively heated by heat lamps. A 1.0-cm^2 polypropylene mesh screen prevented fish from directly contacting the chamber floor and the chamber width allowed stingrays to swim and turn easily. The 8°C temperature range applied over the chamber's length assured that stingrays could experience no greater than a 0.5°C temperature change across their disk width. Flow and chamber orientation effects that might influence stingray preference for a particular chamber location were minimized by maintaining a low flow rate, and by reversing the direction of flow through the apparatus between trials (Coutant, 1977).

Temperature preference was determined for ten ribbontail stingrays with disk widths between 10.3 and 15.4 cm and masses between 85.2 and 227.3 g. Water temperatures selected by each fish were monitored by suturing an iButton® temperature logger (Model # DS1922L) to the right, dorsal aspect of the pectoral disk, ~7 cm from the outer edge. It was not necessary to use anesthesia as loggers could be attached quickly (less than 1 min) through the disk margin with a single suture. Temperature loggers were small (1.5-cm diameter and 0.5-cm height; 3.2 g) comprising less than 2% of the fish's total body weight. Loggers recorded temperatures (±0.13°C) at 5 -min intervals. For each trial, a single stingray was placed into the thermal gradient chamber, and data collection started after the first hour. Water temperatures were then logged over the following 24-h period. Mean, median, and modal temperatures were determined from the logger data for each stingray, and all three endpoints for the population were estimated as the grand mean of the individual mean values (Reynolds & Casterlin, 1979).

Upper and lower chronic temperature trials

The thermal acclimation range of the ribbontail stingray was estimated from chronic upper and chronic lower temperatures measured using a modification of the chronic lethal methodology described by Beitinger et al. (2000). Briefly, ten stingrays selected randomly from the holding tank were placed, one each, into biologically filtered, 100-l chronic treatment aquaria at 26°C. Temperature in five of the treatment aquaria was increased 1°C per day until stingrays stopped feeding. The mean feeding cessation temperature of the group ($n = 5$) was taken as the chronic upper temperature. A chronic lower limit was similarly determined except that temperatures were reduced by 1°C per day in the remaining five treatment aquaria.

Upper and lower temperature tolerance trials

Upper and lower temperature tolerance values were determined from four or five replicate groups of two ribbontail stingrays acclimated at 20.9, 27.2, 29.9, or 32.0°C for 12 days. For each temperature treatment replicate, two randomly selected stingrays were transferred from the holding tank into a biological filtered, 160-l acclimation aquarium at 26°C. One stingray in each acclimation aquarium was used in an upper temperature tolerance trial; the other was used in a low-temperature tolerance trial. The acclimation process was initiated by increasing or decreasing aquarium temperatures by 1°C per day, until the appropriate treatment temperature was reached. Stingrays were then held for an additional 12 days before undergoing temperature tolerance trials. Although no data exist for elasmobranch fishes, bony fishes have been shown to make all, or nearly all acclimation adjustments within 10 days (Sumner & Doudoroff, 1938; Chung, 1980; Bennett et al., 1998). The holding tank feeding regimen of chopped tuna offered on alternate days was continued during the acclimation period; however, stingrays were not fed 48 h in advance of, or during experimental trials.

Temperature tolerance values were estimated as critical thermal maximum (CTmax) or critical thermal minimum (CTmin) temperatures, and were derived using the critical thermal methodology originally described by Cowles & Bogert (1944), and later adapted for fish (Becker & Genoway, 1979; Paladino et al., 1980; Beitinger et al., 2000). For each critical thermal trial, a stingray from the appropriate acclimation treatment aquaria was placed into an insulated 45 × 30 × 15 cm temperature tolerance chamber. The chamber consisted of a 15 l recirculating seawater bath that could be heated with two 350-W submersible aquarium heaters or chilled using an Aqua Euro USA Max Chill Aquarium Chiller (¼ horsepower) at a constant rate of 0.25°C/min (Cox, 1974; Becker & Genoway, 1979; Fangue & Bennett, 2003). Water temperature change continued until tetanic contraction of the pectoral disk was observed. Onset of tetany was an easily recognized, repeatable, nonlethal endpoint at high and low temperatures (Cox, 1974; Beitinger et al., 2000), and is equivalent to muscle spasm endpoints used in many fish studies (Lutterschmidt & Hutchinson, 1997). Fish were held 24-h post-study to access survivorship and all fish survived temperature tolerance trials. CTmax and CTmin values for each treatment group were calculated as the arithmetic mean of the collective replicate endpoint temperatures (Cox, 1974; Becker & Genoway, 1979; Beitinger et al., 2000). Following each trial, stingrays were weighed (wet mass ± 0.1 g), measured (disk width ± 0.1 cm), and returned to the appropriate acclimation temperature to recover.

Temperature tolerance polygon

The critical and chronic temperature data were used to define the ecological thermal niche for juvenile ribbontail stingrays, graphically expressed as a quadrilateral polygon (Bennett & Beitinger, 1997; Fangue & Bennett, 2003; Eme & Bennett, 2009b). The thermal tolerance polygon was constructed by plotting CTmax and CTmin on acclimation temperature and extrapolating the resulting regression lines outward to the chronic upper and chronic lower temperature limits. The resulting figure was expressed quantitatively using the areal units °C^2. Total polygonal area was further divided into an intrinsic tolerance zone (i.e., thermal tolerance independent of previous thermal acclimation) as well as upper and lower acquired tolerance zones (i.e., thermal tolerance gained through acclimation) by dividing the polygon with horizontal lines originating at the intersection of the CTmin and CTmax regressions at their respective upper and lower chronic limits.

Respirometry trials

Standard flow-through respirometry techniques (Steffensen, 1989; Cech, 1990) were used to determine routine resting metabolic rates of ten ribbontail stingrays. Fish were fasted for 48 h before trials to ensure that measurements were taken in a post-absorptive state (Hopkins & Cech, 1994; Di Santo & Bennett, 2011). In each trial, a stingray was placed into a flow-through respirometer comprised of a high density (1.45 g/cm^3) poly-chloroethanediyl cylinder (30 cm × 28.0 cm outside diameter × 0.9 cm wall thickness) with a 1.3 cm thick Plexiglas® top. The opaque respirometer prevented fish from being disturbed by outside movements, while the clear top allowed fish to be viewed if necessary. Poly-chloroethanediyl is commonly used in the construction of oxygen-measuring systems owing to its negligible oxygen absorption and desorption properties (Stevens, 1992). The respirometer was submerged into a constant temperature water bath, and filtered seawater was supplied to the chamber via a constant-pressure head box. Stingrays were acclimatized to the respirometer for 12 h (Hopkins & Cech, 1994; Neer et al., 2006) before trials. During acclimatization, fully saturated seawater at 27.5°C was allowed to flow freely through the respirometer. At the start of each trial, air pockets were eliminated (Carlson & Parsons, 1999) and respirometer flow rates (l/h) adjusted based on fish body mass so that the difference between inflow and outflow oxygen concentration (mg/l) never fell below 85% saturation (Cech, 1990). Fish were held at the new flow conditions for 1 h, a period necessary to ensure 99% water exchange in the respirometer (Steffensen, 1989). Temperature and oxygen concentrations of inflow and outflow were recorded at 30-min intervals using a Yellow Springs Instruments oxygen meter (model 550A), and oxygen values confirmed by Winkler titration (Cox, 1990).

Stingray metabolic rates were measured at a midpoint temperature of 27.5°C, as well as 30.5 ± 0.25 and 24.5 ± 0.25°C. To avoid directional thermal effects, metabolic rates for five of the stingrays were determined four times: (1) at the midpoint temperature, (2) following an acute 3°C decrease, (3) again at the midpoint temperature, and (4) after an acute 3°C temperature increase. Metabolic rates for the remaining five stingrays were determined by subjecting fish to the reciprocal temperature sequence, i.e., mid–high–mid–low temperature exposure. Oxygen uptake measurements at each of the three temperature treatments were recorded for at least 3 h before increasing or decreasing temperature. The respirometer, including tubing and head box, was thoroughly washed with antibacterial soap and left to air dry between trails. A blank respirometry trial (identical in all respects but without the stingray) was run after the fifth and tenth trial and the mean blank value used to correct for non-fish oxygen uptake. Total oxygen consumption rates were calculated from the equation (Cech, 1990):

$$\text{Total resting routine oxygen uptake} = (O_{2_\mathrm{i}} - O_{2_\mathrm{f}}) \times \dot{V}_\mathrm{w}$$

where O_{2_i} the is oxygen concentration of inflow water (mg/l), O_{2_f} is the oxygen concentration of outflow water (mg/l), and $\dot{V}_\mathrm{w}$ is water flow rate through the respirometer (l/min). All values were corrected for non-fish respiration by subtracting the treatment blank value from the total. Metabolic rate data were reported in two ways; total rate of oxygen consumption during a trial, as well as mass-independent metabolic rate adjusted using a scaling exponent of 0.67, consistent with much of the elasmobranch literature (Hopkins &

Cech, 1994; Meloni et al., 2002; Di Santo & Bennett, 2011).

Metabolic temperature sensitivity (Q_{10})

Temperature quotients were used to assess temperature effects on total metabolic rate. This index of thermal sensitivity was estimated from average metabolic rates of all stingrays acutely exposed to temperature changes of 27.5–24.5, 27.5–30.5, and 24.5–30.5°C. All Q_{10} values were determined using the following 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 the mean metabolic rates at temperatures T_2 (high temperature) and T_1 (low temperature), respectively.

Statistical analyses

Simple linear regression analysis (SLR) was used to test relationships between acclimation temperature and CTmin or CTmax. Analysis of covariance with body mass as the continuous predictor variable and acclimation temperature as the categorical predictor variable was used to look for mass effects on CTmin and CTmax values.

The relationship between mean metabolic rates measured at 24.5, 27.5, and 30.5°C was tested using repeated measures Analysis of variance (ANOVA) with relationships between mean values examined using Tukey's multiple range test (MRT). Statistical decisions were based on an alpha level of 0.05. All values are given as mean ± 1 standard deviation.

Results

Temperature preference data

When placed into the thermal gradient, ribbontail stingrays moved randomly along the chamber length for approximately an hour or less before settling. After this time a substantially reduced range of temperatures were visited by the fish. All stingrays demonstrated similar exploratory behavior, and analysis of temperatures selected by individual fish showed that each visited a range of temperatures between 32.8 (±1.86) and 24.6 (±0.65)°C while in the thermal gradient. Even though the thermal gradient shifted slightly from daytime to nighttime due to fluctuations in environmental temperature, fish demonstrated high fidelity to their preferred temperature suggesting that they were responding to thermal cues and not chamber characteristics. Once at their preferred temperature stingrays remained relatively quiescent over the remainder of the trial period. Grand mean, median, and modal temperatures, calculated from the individual mean values were 28.0 (±0.71), 28.2 (±0.61), and 28.1 (±0.69)°C, respectively, and differed by no more than 0.2°C across trials.

Thermal tolerance polygon data

Critical thermal minima and maxima of fish in temperature tolerance trials were insensitive to changes in mass. Analysis of covariance with body mass as the covariate returned adjusted least-square mean values that differed by no more than 0.18°C from CTmin and 0.03°C from CTmax values that were empirically determined. Because differences between measured and adjusted tolerance values were negligible, measured values were used in calculating thermal polygon areas as well as the linear regression predictive models.

The upper and lower critical and chronic thermal limits of juvenile ribbontail stingrays revealed a relatively orthogonal thermal niche (Fig. 1). The range of acclimation for the species, estimated from upper and lower feeding cessation temperatures, was between 16.8 and 34.0°C, resulting in a total acclimation scope of 17.2°C. Stingrays acclimated at temperatures within their acclimation zone (20.9–32.0°C) exhibited CTmax ranging between 39.0 and 40.9°C (Table 1). Regression analysis found a highly significant relationship between acclimation temperature and CTmax values (SLR; $F_{1,16} = 35.26$; $P < 0.0001$) defined by the following model:

$$\text{CTmax } (^\circ\text{C}) = 35.860 + \text{Acclimation Temperature } (^\circ\text{C}) \times 0.155.$$

The r^2 value for the model indicates that 68.8% of the variability in the critical thermal maxima is explained by changes in acclimation temperature.

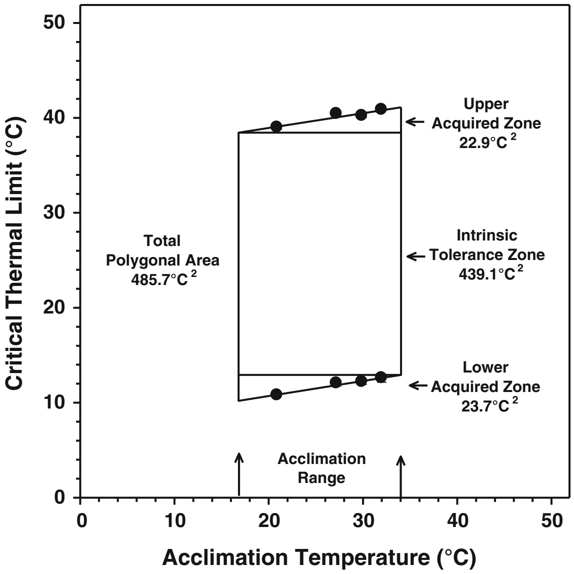

Fig. 1 Thermal tolerance polygon for juvenile ribbontail stingrays, *Taeniura lymma* (Forsskål, 1775), from a Hoga Island nursery, southeast Sulawesi, Indonesia. The polygon is constructed from upper chronic and critical thermal maxima, and lower chronic and critical thermal minima measured across this species' acclimation range. The thermal tolerance area is divided into intrinsic as well as upper and lower acquired tolerance zones. Each zone is quantified by its area expressed as °C^2. See text for detailed description

The acclimation response ratio (i.e., the slope of CTmax or CTmin on acclimation temperature) was significantly greater than zero, and revealed ribbontail stingrays accrue 0.16°C of heat tolerance for every 1°C increase in acclimation temperature. Similarly, regression analysis of CTmin (range = 10.8–12.6°C) on acclimation temperature found a highly significant relationship (SLR; $F_{1,17} = 24.51$; $P < 0.0001$) defined by the equation:

$$\text{CTmin}\,(^\circ\text{C}) = 7.484 + \text{Acclimation Temperature}\,(^\circ\text{C}) \times 0.160.$$

The r^2 value for the CTmin model indicates that 59.0% of cold tolerance variation is accounted for by acclimation temperature. The acclimation response ratio for cold tolerance was equivalent to the heat tolerance response with stingrays gaining 0.16°C of cold tolerance for every degree decrease in acclimation temperature. A thermal tolerance polygon constructed from chronic and critical temperatures revealed relatively small zones of upper and lower acquired tolerance nearly identical in size with a combined area of 46.6°C^2 or 9.6% of the total polygonal area. The thermal niche, however, is dominated by an intrinsic tolerance zone comprising 90.4% of the total polygonal area.

Respirometry trials

Resting routine metabolic rates of ribbontail stingrays were strongly influenced by changes in temperature, with total metabolic rates ranging from 18.38 to 39.10 mgO$_2$/h, and mass-independent rates ranging between 0.51 and 1.18 mgO$_2$/h/g$^{0.67}$ at water temperatures between 24.5 and 30.5°C, respectively (Table 2). Significant differences in total metabolic rate were apparent at all temperature change treatments. A repeated measures ANOVA revealed significant differences in mass-independent metabolic rates

Table 1 Mean (±SD) disk width and wet mass as well as critical and chronic thermal tolerance values for juvenile ribbontail stingrays, *Taeniura lymma* (Forsskål, 1775), acclimated at temperatures between 20.9 and 32.0°C

Acclimation Temperature (°C)	*n*	Disk width (cm)	Wet mass (g)	Critical limit (°C)	Chronic limit (°C)
Thermal minima					
20.9	4	14.1 (±1.83)	163.0 (±58.44)	10.8 (±0.23)	16.8 ($n = 5$)
27.2	5	12.7 (±2.16)	136.1 (±46.58)	12.1 (±0.77)	
29.9	5	15.4 (±1.91)	209.8 (±84.10)	12.2 (±0.59)	
32.0	4	14.4 (± 4.60)	180.0 (± 142.83)	12.6 (± 0.85)	
Thermal maxima					
20.9	4	16.0 (±3.46)	241.0 (±104.80)	39.0 (±0.35)	34.0 ($n = 5$)
27.2	5	14.3 (±1.65)	158.8 (±32.32)	40.4 (±0.52)	
29.9	5	14.7 (±1.27)	170.1 (±44.82)	40.2 (±0.39)	
32.0	4	16.0 (±2.77)	207.5 (±131.24)	40.9 (±0.06)	

Note that the chronic thermal limits denote lower and upper acclimation temperatures and are not associated with an acclimation treatment group

Table 2 Average (±SD) wet mass, disk width, total routine resting, and mass-independent metabolic rates for ten juvenile ribbontail stingrays, *Taeniura lymma* (Forsskål, 1775), acclimated at 27.5°C and exposed to an acute temperature increase and decrease to 24.5 and 30.5°C, respectively

n	Wet mass (g)	Disk width (cm)	Temperature (°C)	Metabolic rate		Q_{10}	
				Total (mg/h)	Mass-independent (mg/h)	Treatment	Value
10	184.7 (± 48.75)	15.3 (±1.24)	24.5 (low)	18.38 (±9.722)	0.51 (±0.185)	Low ← mid	6.02
			27.5 (mid)	30.47 (±9.340)	0.94 (±0.266)	Mid → high	2.16
			30.5 (high)	39.10 (±9.776)	1.18 (±0.176)	Low ↔ high	3.48

Temperature quotients (Q_{10}) are given for fish transferred between low, mid and high temperature treatments, and were calculated from total metabolic rate values

measured at temperatures of 24.5, 27.5, and 30.5°C ($F_{3,1} = 16.38$; $P < 0.0001$). Tukey's MRT found significant differences between metabolic measures at all three treatment temperatures ($\alpha = 0.05$).

While total metabolic rates exhibited significant differences regardless of the direction of temperature change, the magnitude of the metabolic responses was disproportional (Fig. 2). Whereas stingrays subjected to an acute temperature increase from 27.5 to 30.5°C doubled their metabolic rate, those acutely exposed to a temperature drop from 27.5 to 24.5°C, showed a six-fold decrease in total routine oxygen uptake. In both cases, the change in total routine resting metabolic rate was highly significant (ANOVA; $F_{3,1} = 16.38$; $P < 0.0001$). The temperature quotient value estimated across the entire six degree shift had an intermediate Q_{10} of ~ 3. The disproportional metabolic responses were not likely directional artifacts. Student's *t* test found no significant differences when mid-temperature (27.5°C) metabolic rates taken at the start of each study were compared to those measured following an acute temperature increase or decrease ($T_8 = 1.06$; $P = 0.311$).

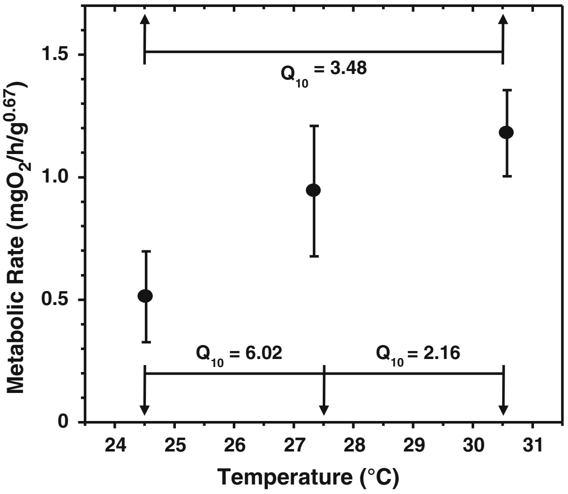

Fig. 2 Mean mass-independent metabolic rates (mgO$_2$/h/g$^{0.67}$) for juvenile ribbontail stingrays, *Taeniura lymma* (Forsskål, 1775) at 24.5, 27.5, and 30.5°C. All values are given as mean ± 1 standard deviation. Temperature quotients (Q_{10}) are calculated from metabolic rates across temperatures indicated by the arrows on the upper and lower *X*-axes

Discussion

When given a range of water temperatures to choose from, ribbontail stingrays are capable of distinguishing their thermal preferendum (28.4°C) with a remarkable degree of fidelity. Juveniles were highly discriminative of their experimental thermal environment, and exhibited thermal preferenda varying less than 0.7°C between individuals. Even while temperatures in some parts of their nursery may exceed the fish's heat tolerance limits (Taylor et al., 2005), perhaps ribbontail stingrays avoid dangerous thermal extremes by following subtle thermal gradients to remain at more amenable temperatures (Bennett, 2010). A high level of thermal discrimination is likely necessary for juvenile rays to successfully negotiate dynamic thermal conditions that change nearly continuously in relation to tidal movement and time of day (i.e., insolation level). Thermal preference studies in elasmobranchs are rare with thermal preferenda known for only three eurythermic species, the dusky smoothhound, horn shark, and the Atlantic stingray. Preferred temperatures for the more stenothermic juvenile ribbontail stingray are higher, and also less variable than those of other elasmobranchs tested to date. Values from previous studies vary among their respective species based on time of day (Casterlin & Reynolds, 1979), hypothalamic temperature (Crawshaw & Hammel, 1973), as well as parturition and prandial state (Wallman & Bennett, 2006). Dusky smooth-hound showed a bimodal distribution in preferred temperatures with slightly warmer crepuscular preferred temperatures and an average preferenda of ~27°C. Temperatures preferred by juvenile horn sharks never exceeded 26°C even when the brainstem was cooled to temperature as low as 12°C, and Atlantic stingray showed relatively variable thermal preference values with males and non-pregnant females having a median temperature preference of 25.3 and 26.8°C, respectively. By comparison juvenile ribbontail stingrays exhibit a temperature preference between 1.5 and 3.0°C higher than other elasmobranchs tested to date.

The fundamental thermal niche of juvenile ribbontail stingrays is indicative of a warm tolerant species that experiences little change in ambient water temperature. Compared to the Atlantic stingray, juvenile ribbontail stingrays exhibit a polygon that is shifted toward higher temperatures on both axes (i.e., upward and to the right). Stated another way, ribbontail rays have a thermal niche characterized by a narrow but markedly high range of acclimation temperatures and elevated high and low thermal tolerance values (Fig. 1). Given their limited acclimation ability, it is perhaps not surprising that ribbontail stingrays move with the tides to avoid being stranded in isolated pools where temperatures can reach near lethal levels (Taylor et al., 2005; Eme & Bennett, 2009a; Bennett, 2010). By following the tide, fish experience relatively constant diel temperature conditions regardless of tidal stage. Similarly, juvenile stingrays see little change in water temperature between wet and dry seasons throughout their tropical western Pacific range. The fish have a relatively small polygon with the acquired upper and lower thermal tolerance zones accounting for less than 10% of their thermal niche, a conformation suggesting a minimal ability to acquire additional heat or cold tolerance through acclimation. Accordingly, juvenile ribbontail stingrays demonstrate a low acclimation response ratio (0.16°C change in tolerance for every 1°C change in acclimation temperature). Conversely, Atlantic stingrays display a more typical eurythermic polygonal pattern, gaining 30% of their tolerance through acclimation (acclimation response ratio = 0.31 for heat tolerance and 0.41 for cold tolerance) and boasting a polygonal area of 978°C^2, the third largest known among fishes (Fangue & Bennett, 2003). This species, in contrast to the ribbontail stingray, is well suited to large seasonal temperature shifts with water temperatures falling as low as 2°C in winter and increasing to upwards of 36°C by mid-summer.

Ribbontail stingray temperature quotients reveal an interesting dichotomy, whereby an acute temperature increase resulted in a doubling of metabolic rate, but a similar temperature decrease produced a six-fold drop in metabolism. While exponential metabolic increases are the typical ectotherm response to rapid temperature increase (Schmidt-Nielsen, 1997), this strategy is unsustainable for fish living in shallow intertidal zones that experience daily extremes. Indeed, resident fishes that remain in isolated nursery area pools during daytime low tide often exhibit compensatory adaptations to limit metabolic costs. For example, common goby, *Bathygobius fuscus* (Rüppell, 1830), and the undescribed sandflat goby, *Bathygobious* sp., both resident to Hoga Island mangals, show no metabolic increase even as tidepool temperatures approach 40°C (Eme & Bennett, 2009a). These gobies support enzymatic pathways that function across a wide temperature range and exhibit temperature quotients of 1.0, a phenomenon referred to as instantaneous compensation (Newell & Northcroft, 1967). Ribbontail stingrays, on the other hand, avoid energetic expenses associated with warm temperatures during low tide by moving to more amenable temperatures as tides recede (Bennett, 2010). It is less clear, however, how stingrays benefit from the dramatic decrease in metabolism at temperatures below 26°C. Similar cold exposure Q_{10} values were reported by Hopkins & Cech (1994) for the bat ray, *Myliobatis californica* (Gill, 1865), which experienced a nearly seven-fold decrease in metabolic rate when moved from 20 to 14°C. It was postulated that bat rays benefit from this response by feeding in warm water and then moving to cooler temperatures where digestion efficiency is increased as evacuation rates slow allowing food to remain on digestive surfaces longer (Sims et al., 2006). For small juvenile ribbontail rays, however, moving to cooler deeper waters would likely take them away from sheltered nursery areas, thereby increasing predator exposure. The steep metabolic decline more likely acts as a classic directing factor steering stingrays to warmer more bioenergetically optimal temperatures (Fry, 1947, 1971). Interestingly, both high and low temperature effects on metabolic rate reinforce the narrow thermal niche and extreme thermal fidelity seen in juvenile ribbontail stingrays.

While juvenile ribbontail stingrays are well suited to shallow intertidal areas (Chin et al., 2010), adults inhabit cooler deeper waters off the reef crest (O'Shea et al., 2011). Reef temperatures at our study site typically ranged between 20 and 25°C, thermal conditions avoided by juvenile ribbontail stingrays. It would appear differing temperature requirements can be an effective mechanism for separating adults from juveniles in areas where persistent and predictable thermal heterogeneity exists. Ontogenetic shifts in thermal preferences have been identified in several marine bony fish species, but our data are the first to suggest this phenomenon for an elasmobranch species. Juvenile bony fish commonly exhibit warmer thermal preferenda than adults (McCauley & Huggins, 1979), some examples include: striped bass, *Morone saxatilis* (Walbaum, 1792), (Coutant, 1985; Zale et al., 1990), gizzard shad, *Dorosoma cepedianum* (Lesueur, 1818), (Gebhart & Summerfelt, 1978), blueback herring, *Alosa aestivalis* (Mitchill, 1814), (Nestler et al., 2002) rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792), (Fast, 1973; Rowe & Chisnall, 1995), kokanee, *Oncorhynchus nerka* (Walbaum, 1792), (Berge, 2009) and cutthroat trout, *Oncorhynchus clarki* (Richardson, 1836), (Baldwin et al., 2002). In all cases, juveniles preferred waters 2 to 4°C warmer than adults, about the same temperature difference seen between juvenile and adult ribbontail stingray habitats. Differing thermal distributions may be necessary for species such as ribbontail stingrays where juveniles require shallow conditions that are inaccessible to larger predators, or to exploit prey common to warmer nursery areas. The benefits to juvenile rays likely include increased survival, reduced competition and faster growth during their early life history. Prior to recruiting to cooler reef habitats, juveniles likely undergo an ontogenetic shift in thermal physiology requiring remodeling of biochemical pathways to improve physiological function at cooler reef temperatures.

Tolerance, preference, and metabolic data all suggest that juvenile stingrays are physiologically suited to a well-defined, if somewhat narrow range of environmental temperatures. These same data may also provide useful insights into how ribbontail stingrays may respond to long-term shifts in the region's climate. Mean monthly Indo-Pacific sea surface temperatures (range = 30.5–37.3°C between 1981 and 2004; Richard Reynolds, NOAA, personal communication) already closely approach the stingray's thermal tolerance limits. With sea surface temperatures predicted to increase by ~2°C over the next 50 years (IPCC, 2007; Poloczanska et al., 2007), it seems possible that stingrays living in nursery areas will be adversely affected. Concerns over how fish populations might be affected by global climate change have largely looked at open ocean systems (Perry et al., 2005; Portner & Knust, 2007; Portner & Farrell, 2008) with little emphasis placed on how climate change will affect fringing reef nurseries (Wilson et al., 2010). An increase in peak temperatures, while not immediately lethal, may shift stingray distributions away from traditional nurseries and into deeper water as fish seek out their preferred niche temperatures. Juveniles could no doubt find more amenable thermal conditions, but would do so at the risk of increasing predation pressure as well as greater competition for food and shelter. A likely outcome would be to increase pressure on top predator populations already threatened by reef degradation and over-fishing (Teh et al., 2005; White & Dharmadi, 2007) as well as possible changes to reef and nursery benthic trophic structure (Munday et al., 2008).

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