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Aerobic response to thermal stress across ontogeny and habitats in a teleost fish

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Abstract

Near-future climate change projections predict an increase in sea surface temperature that is expected to have significant and rapid effects on marine ectotherms, potentially affecting a number of critical life processes. Some habitats also undergo more thermal variability than others, and the inhabitants therefore must be more tolerant to acute periods of extreme temperatures. Mitigation of these outcomes may occur through acclimation, plasticity or adaptation, although the rate and extent of a species' ability to adjust to warmer temperatures is largely unknown, specifically as it pertains to effects on various performance metrics in fishes that inhabit multiple habitats throughout ontogenetic stages. Here, the thermal tolerance and aerobic performance of schoolmaster snapper (*Lutjanus apodus* Walbaum, 1792) collected from two different habitats were experimentally assessed under different warming scenarios (temperature treatments = 30, 33, 35, 36°C) to assess vulnerability to an imminently changing thermal habitat. Larger subadult and adult fish collected from a 12 m deep coral reef exhibited a lower critical thermal maximum (CT_{max}) compared to smaller juvenile fish collected from a 1 m deep mangrove creek. However, the CT_{max} of the creek-sampled fish was only 2°C above the maximum water temperature measured in the habitat from which they were collected, compared to a CT_{max} that was 8°C higher in the reef-sampled fish, resulting in a wider thermal safety margin at the reef site. A generalized linear model showed a marginally significant effect of temperature treatment on resting metabolic rate (RMR), but there were no effects of any of the tested factors on maximum metabolic rate or absolute aerobic scope. *Post hoc* tests revealed that RMR was significantly higher for creek-collected fish at the 36°C treatment and significantly higher for reef-collected fish at 35°C. Swimming performance [measured by critical swimming speed] was significantly lower at the highest temperature treatment for creek-collected fish and trended down with each successive increase in temperature treatment for reef-collected fish. These results show that metabolic rate and swimming performance responses to thermal challenges are somewhat consistent across collection habitats, and this species may be susceptible to unique types of thermal risk depending on its habitat. We show the importance of intraspecific studies that couple habitat profiles and performance metrics to better understand possible outcomes under thermal stress.

1 | INTRODUCTION

Climate change projections outlined by the Intergovernmental Panel on Climate Change (IPCC) predict that global sea surface temperatures will increase by 2 to 4°C by 2100 based on various emissions scenarios (Hoegh-Guldberg et al., 2014). This warming is expected to have significant and rapid effects on marine ectotherms (Pörtner & Farrell, 2008; Poloczanska et al., 2016; Sunday et al., 2012). In fishes, documented and predicted detrimental effects of warming can alter individual performance and ultimately affect biological communities and ecosystems (Farrell, 2009; Madeira et al., 2017; Robinson et al., 2019; Slesinger et al., 2019). Thermal stress has been shown to negatively affect a number of critical life processes, including reproduction (Donelson et al., 2014), growth rate (Grans et al., 2014) and aerobic performance (Jensen et al., 2017; Nilsson et al., 2009; Rummer et al., 2014), and effects may differ throughout an individual's life. Stress responses may be mitigated through acclimation, plasticity, adaptation, migration or a combination thereof (Culumber & Monks, 2014; Donelson et al., 2010; Madeira et al., 2017; Somero, 2010), but the extent of a species' ability to adjust to a warmer environment, and the rate of potential adaptation, is largely unknown.

While the effects of thermal stress have been studied across marine taxa and habitats, an important yet understudied subset of investigations is still developing on how thermal stress will affect individual species across life stages that occupy different habitats. Evidence suggests that crustacean species inhabiting thermally variable intertidal habitats are less resilient to thermal stress than closely related congeneric species inhabiting more thermally stable areas (Somero, 2010), but few similar studies exist that examine a single ontogenetically separated species. Many fish species utilize several habitats throughout their lives (Galaiduk et al., 2017; Lee et al., 2019; Schlosser, 1991), and this spatial variance can result in a bottleneck occurring at one or more life stages as extreme temperature events often affect habitats differently (e.g., Lindmark et al., 2018). If various life stages of a given species were to occur through different habitats, it is likely that studying a single stage will not provide a full understanding of that species' susceptibility to thermal stress (Dahlke et al., 2020), therefore intraspecific investigations coupling habitat profiles, performance metrics and thermal sensitivity have the potential to enable better understanding of possible outcomes under various abiotic fluctuations such as heat waves.

The schoolmaster snapper (Lutjanus apodus Walbaum, 1792) is a subtropical marine fish that inhabits shallow, nearshore areas, such as mangrove creeks, during its juvenile stage and deeper reef environments during its adult stage, a characteristic of many warm-water marine fishes (Igulu et al., 2014). This species typically separates by life stage (Verweij et al., 2007) and does so for a number of reasons, including optimal prey availability or predator avoidance (Nagelkerken, 2009), but the thermally distinct habitats that they segregate into may create fitness bottlenecks for a population. Assessing performance across habitat (i.e., ontogeny in this example) may therefore potentially be useful in predicting any responses to thermal stress, especially as documentation of migration of juvenile fish populations to avoid stressors in their nearshore environments has only recently begun to come to light (e.g., Bangley et al., 2018; Tanaka et al., 2021). Additionally, this species may act as a model for understanding the responses of other ecologically and economically important subtropical marine organisms.

Here, we define the thermal tolerance and aerobic performance of two spatially and thermally distinct life stages of L. apodus and link this tolerance to in situ monitoring of ocean temperatures from collection sites. By exposing fish to a range of elevated sea surface temperatures, we assess each ontogenetic stage's susceptibility to thermal stress based on their contemporary habitat.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

The care and use of experimental animals complied with American and Bahamian animal welfare laws, guidelines and policies as approved by the University of Illinois (IACUC Protocol #14133) and the Bahamian Department of Marine Resources (permit MAMR/FIS/17).

2.2 | Fish collection

This study took place at the Cape Eleuthera Institute (CEI), The Bahamas (24°49′46″N, 76°19′42″W). Lutjanus apodus were caught using baited traps or a cast net in a shallow mangrove creek [<1 m depth, Page Creek, South Eleuthera; 11.0–18.3 cm total length (TL)] and using rod and reel on a coral reef (12 m depth, "Cathedral Reef", South Eleuthera; 28.0–43.6 cm TL). Fish collected from the deeper reef site were placed in a wire cage after landing and immediately lowered to 5 m to alleviate barotrauma (Drumhiller et al., 2014), then slowly brought to the surface after a period of 20 min. All fish were transported in 113 L coolers by boat to the CEI wetlab. Water changes were performed every 5 min to ensure adequate aeration and optimal water quality (Murchie et al., 2009). Larger reef fish were held in 13,180 L cylindrical tanks and smaller creek fish in 454 L raceway tanks for no longer than 2 weeks prior to experimentation. Fish were fed chopped sardines (Sardinella aurita) to satiation daily and kept under a natural light–dark cycle in the outdoor, covered wetlab.

All tanks were continuously supplied with fresh seawater pumped from a nearshore area, and no effort was made to control any variation in temperature prior to experimentation that may have occurred naturally due to diel/tidal fluctuations.

2.3 | Habitat temperature monitoring

Temperature loggers (DS1921H Thermochron iButton High Resolution, Maxim Integrated, San Jose, CA, USA) were deployed in each fish collection location, and the temperature logged hourly for 6 months, spanning the experimental timeframe. The temperature logger deployed in the creek habitat was affixed to a mangrove root, and another logger was deployed at the base of the mooring at the collection reef.

2.4 | Critical thermal maximum (CT$_{max}$)

Following capture and holding tank acclimation to ambient conditions for 1 week, critical thermal maximum was measured for eight creek fish (11–15.2 cm, mean = 12.9 cm) and eight reef fish (31.9–42.7 cm, mean = 37 cm) using methods adapted from Murchie et al. (2011). Each fish was placed into an individual 10 L flow-through aquarium seated in a raceway. Each aquarium was aerated and supplied with seawater recirculated from a reservoir at the end of the raceway. Water temperature was increased from ambient (mean 30.2°C) at a rate of 0.1°C min^{-1} using an immersion heater (43 cm heater, model ESA1.8117-P1, 120 V, 1800 W; Process Technology, Willoughby, Ohio, USA) controlled by a digital thermostat (model DRAE 15–1, 120 V; DRA Series LCD; Process Technology, Willoughby, Ohio, USA) placed in the raceway. On loss of equilibrium, temperature and dissolved oxygen were recorded in each aquarium, and the fish were removed and re-acclimated to ambient conditions for at least 24 h then released at their capture location. These fish were not re-used for aerobic performance trials.

2.5 | Aerobic performance

Fish used in the aerobic performance testing were collected and transported to the laboratory using methods identical to those described above. Once at the laboratory, fish were placed in flow-through acclimation tanks supplied continuously with fresh seawater, and the temperature was adjusted and maintained at one of four treatment levels (30, 33, 35 or 36°C) over the course of 24 h [see Munday et al. (2009) for the rate of temperature increase]. A temperature of 30°C was selected as the first treatment to provide a close approximation of the mean summertime temperature measured in the two fish collection habitats, and the additional treatments were derived from field monitoring at the collection sites. Fish were held and fed at treatment temperatures for 7 days because when working at these elevated temperatures additional acclimation time has been shown to not alter experimental

outcomes in other marine species (Munday et al., 2009). Food was then withheld for 24 h prior to testing to ensure a post-absorptive state was reached before measuring metabolic rates (Jain et al., 1997; Roche et al., 2013). An individual fish was moved into a swim tunnel respirometer with fresh flow-through seawater adjusted to the respective acclimation temperature and flushed at a speed of 1 cm s^{-1} for an overnight acclimation (43 cm heater, model: ESA1.8117-P1, 120 V, 1800 W; Immersion Process Technology). Water supplied to the swim tunnels was filtered mechanically with a series of bag filters down to 25 μm and was run through an in-line ultraviolet radiation filter. The respirometer was covered with a tarpaulin to avoid any visual disturbance. Reef-collected fish (n = 7 per treatment, 28–43.6 cm, mean = 34.4 cm) were tested in a cylindrical Blazka-type swim tunnel respirometer (volume = 108.74 L, internal dimensions 100 cm long × 31.9 cm diameter; diagram included in Thorstad et al., 1997). The impellor was powered by a Leeson Washguard three-phase AC motor (model C182T17WK3D; Leeson Electric; Grafton, Wisconsin, USA) and controlled by a Leeson Speedmaster motor controller (model 174526, 0–120 Hz; Grafton, Wisconsin, USA). Creek-collected fish (n = 7 per treatment, 13.1–18.3 cm, mean = 15.1 cm) were tested in a Steffensen-type swim tunnel (volume = 30 L, test chamber dimensions 55 cm L × 14 cm W × 14 cm H; Loligo Systems; Viborg, Denmark), powered by a Sew-Eurodrive three-phase AC motor (series DRS71S4/FI/ACE1/EI72; Sew-Eurodrive, Lyman, South Carolina, USA), and a Sew-Eurodrive controller (model IP55 NEMA 12; Sew-Eurodrive; Lyman, South Carolina, USA). At dawn following the acclimation period, resting metabolic rate (RMR) was measured using a 10 min closed measurement period, followed by a 5 min flush period. This cycle was repeated three times. When calculating O$_2$ consumption, linear regressions were fit and the lowest rate was selected ($r^2 \geq 0.95$).

Following the RMR measurement, critical swimming speed (U$_{crit}$) protocols were used to measure swimming performance and maximum metabolic rate (MMR), from which absolute aerobic scope (AAS) can also be calculated (Brett, 1964; Tierney, 2011; Eliason et al., 2013; Roche et al., 2013). Briefly, velocity was increased stepwise by increments of 15 cm s^{-1} every 15 min. During each 15 min interval, a 10 min closed period of measurement was followed by a 5 min flush period to replenish dissolved oxygen. The trial ended with fish 'failure' or exhaustion, indicated by the caudal fin continuously contacting the rear grate of the swim tunnel for 20 s or the fish being forcibly pinned sideways against the grate, as in Lee et al. (2003). The MMR value from the highest velocity increment with an acceptable regression fit was used ($r^2 \geq 0.95$; Svendsen et al., 2016). AAS was calculated by subtracting RMR from MMR, and factorial aerobic scope (FAS) is MMR divided by RMR. U$_{crit}$ was calculated using:

$$U_{crit} = U_f + (t_f/t_i)U_i$$

where U$_f$ is the water velocity of the final completed increment, t$_f$ is the time swum at the final increment, t$_i$ is the incremental time period and U$_i$ is the incremental water velocity (Brett, 1964). In calculating

U_{crit}, the solid blocking factor was incorporated into the calculations for all fish (Bell & Terhune, 1970). After experimentation, all fish were released alive in their respective collection locations.

2.6 | Data analysis

CT_{max} failed assumptions of normality and was log-transformed. A generalized linear model was used to define the effects of total length, habitat (creek vs. reef), and their interaction on log-transformed CT_{max} values (significance level = 0.05, r package lme4). This full model was reduced using backwards stepwise elimination until the minimal adequate model remained, which included only significant terms that caused an increase in AIC when removed (Crawley, 2007).

Each metabolic rate measurement was adjusted for the mass of the fish to be able to analyse the effects of habitat (regardless of the effect of mass) on their response to various temperatures. This was done by fitting a linear regression to each group of absolute whole-animal oxygen consumption data points within a metabolic measure by temperature combination (e.g., MMR at 33°C for creek and reef fish combined) and using the slope of the regression as a scaling exponent applied to the mass component of the measurement unit (see Table 1 for scaling exponents used). RMR, MMR and AAS failed assumptions of normality and were log-transformed, and then failed the assumption of homogeneity of variances, therefore a generalized linear model (GLM) was used to determine the effects of the predictor variables (treatment temperature, habitat and their interaction) on RMR, MMR and AAS (significance

TABLE 1 The scaling exponents used to mass-adjust metabolic rate measurements to account for the known effect of mass

Temperature (°C)	RMR	MMR	AAS
30	0.55	0.7	0.76
33	0.42	0.44	0.45
35	0.55	0.66	0.81

Note: Each exponent is the scale of the regression line fit to each group of absolute whole-animal oxygen consumption data points within a metabolic measure by temperature combination. AAS, absolute aerobic scope; MMR, maximum metabolic rate; RMR, resting metabolic rate.

level = 0.05, r package lme4). The 36°C treatment was omitted from this analysis because high mortality during the 7-day acclimation prevented metabolic measurements from occurring on reef fish. Model assumptions were all verified by visually inspecting diagnostic plots of the residuals and outputs are shown in Table 2. For any significant terms in the GLM, one-way ANOVAs followed by Tukey's HSD tests and t-tests were then used to identify differences across temperature treatments and across habitats, respectively. The ANOVAs used to analyse differences in creek fish data included the 36°C treatment.

A nonparametric paired Wilcoxon test was used to analyse the effects of temperature on critical swimming speed. A Brown–Forsythe test showed equal variances and the data failed a Shapiro–Wilk test, validating the use of the Wilcoxon test. A threshold of $\alpha = 0.05$ was used for all tests.

3 | RESULTS

3.1 | Habitat temperature and critical thermal maxima (CT_{max})

Temperature loggers revealed distinct thermal profiles for the two different habitat types in which fish collection occurred. The tidally influenced mangrove creek experienced wide daily temperature variation, whereas the deeper coral reef site experienced a relatively stable thermal profile (Figure 1). The mean temperature recorded at the mangrove site was 29.1°C (±0.05°C), with a maximum of 39.4°C and a minimum of 19.5°C, while the mean temperature at the reef site was 28.7°C (±0.02°C), with a maximum of 31.3°C and a minimum of 25.6°C.

Creek-collected snapper used during the CT_{max} portion of the study ranged from 11 to 15.2 cm (n = 8, mean = 12.9 cm; Figure 2) and had a CT_{max} of 41.2 ± 0.1°C, and reef-collected snapper ranged from 31.9 to 42.7 cm (n = 8, mean = 37 cm) and had a CT_{max} of 39.1 ± 0.5°C. A model that included only total length was the best predictor of CT_{max} (AIC$_{full model}$ = −66.8, AIC$_{reduced model}$ = −69.69; Table 2) and showed a negative relationship between the two variables, indicating a lower CT_{max} in larger fish. The removal of the interaction term from the model precluded the analysis of the effects of size on performance within collection habitat due to a lack of variation (Table 2).

TABLE 2 Model outputs, Akaike's information criterion (AIC) values and AIC weights (w_i) for each generalized linear model (GLM) used to describe CT_{max}

Parameter	Estimate	S.E.	t value	Pr (>|t|)	Model	AIC	w_i
Full model					Full model	−66.8	0.13
Intercept	*3.82*	*0.08*	*46.28*	*6.77E−15*			
Total length	−0.004	0.002	−1.94	0.08			
Habitat (Creek): Total length	0.002	0.01	0.23	0.82	• Habitat: Total length	−68.70	0.33
Habitat (Creek)	−0.07	0.12	−0.61	0.55	• Habitat	−69.69	0.54
Reduced model					Reduced, model	−69.69	0.54
Intercept	*3.75*	*0.01*	*275.38*	*2.00E−16*			
Total length	*−0.002*	*0.0004*	*−4.73*	*0.0003*	• Total length	−56.41	0.00

Note: Significant predictors are italics. Estimates and standard errors (S.E.) are on a log scale.

TABLE 3 Results of generalized linear models used to quantify the effects of habitat (creek, reef), temperature (30, 33, 35, 36°C), and their interaction on resting metabolic rate (RMR), maximum metabolic rate (MMR) and absolute aerobic scope (AAS)

RMR

Deviance residuals

	Minimum	1st Quantile (25%)	Median	3rd Quantile (75%)	Maximum
	−87.556	−23.025	−7.749	25.594	157.223

Coefficients

	Estimate	Standard error	t value	Pr (>|t|)
(Intercept)	−208.751	160.774	−1.298	0.203
Temperature	9.871	4.930	2.002	0.053
Habitat Creek	−69.159	223.249	−0.31	0.759
Temperature: Habitat Creek	2.379	6.863	0.347	0.731

(Dispersion parameter for Gaussian family taken to be 2015.811)

Null deviance: 92263 on 38° of freedom

Residual deviance: 70553 on 35° of freedom

AIC: 413.2

Number of Fisher scoring iterations: 2

MMR

Deviance residuals

	Minimum	1Q	Median	3Q	Maximum
	−164.3	−49.46	−13.23	52.35	257.63

Coefficients

	Estimate	Standard error	t value	Pr (>|t|)
(Intercept)	175.831	327.685	0.537	0.595
Temperature	7.877	10.047	0.784	0.438
Habitat Creek	130.87	455.019	0.288	0.775
Temperature: Habitat Creek	−3.794	13.988	−0.271	0.788

(Dispersion parameter for Gaussian family taken to be 8373.951)

Null deviance: 300140 on 38° of freedom

Residual deviance: 293088 on 35° of freedom

AIC: 468.74

Number of Fisher scoring iterations: 2

AAS

Deviance residuals

	Minimum	1Q	Median	3Q	Maximum
	−224.11	−83.13	−19.5	50.7	366.59

Coefficients

	Estimate	Standard error	t value	Pr (>|t|)
(Intercept)	232.444	466.701	0.498	0.622
Temperature	2.952	14.310	0.206	0.838
Habitat Creek	−85.954	648.055	−0.133	0.895
Temperature: Habitat Creek	3.302	19.922	0.166	0.869

(Dispersion parameter for Gaussian family taken to be 16,986.13)

Null deviance: 602745 on 38° of freedom

Residual deviance: 594515 on 35° of freedom

AIC: 496.32

Number of Fisher scoring iterations: 2

Note: Significant terms are indicated in italics. 1st Quantile = 25%, 3rd Quantile = 75%.

FIGURE 1 Temperature recorded hourly at each of the fish collection locations, with the black line measured in the mangrove creek collection habitat (mean = 29.1°C, minimum = 19.5°C, maximum = 39.4°C) and the inset grey line measured on the deeper coral reef collection habitat (mean = 28.7 C, minimum = 25.6°C, maximum = 31.3°C). The horizontal lines at the top of the figure represent the measured CT_{max} for creek and reef fish. ——, mangrove creek; ·····, coral reef.
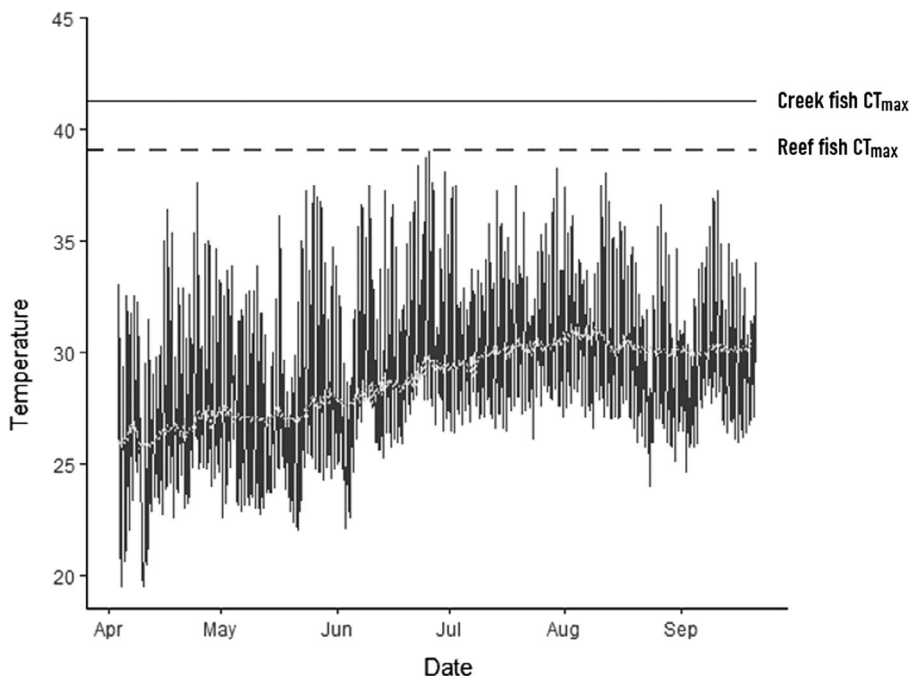
FIGURE 2 Critical thermal maximum (CT_{max}) for creek fish (triangles) and reef fish (circles) of different total lengths. ▲, creek; ●, reef.
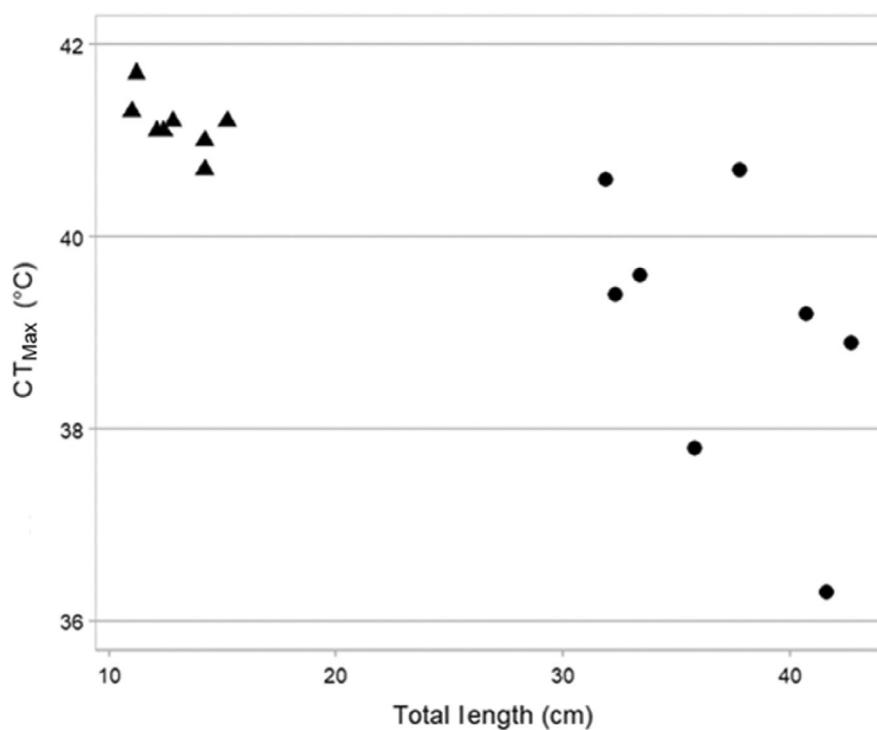
The CT_{max} of the creek fish was only 1.8°C above the maximum water temperature measured at that site, whereas the CT_{max} of reef fish was 7.8°C above their maximum habitat temperature.

3.2 | Aerobic performance

Creek-collected snapper used during the aerobic performance portion of the study ranged from 13.1 to 18.3 cm (n = 29, mean = 15.1 cm), and

reef-collected snapper ranged from 28 to 43.6 cm (n = 20, mean = 34.4 cm). A GLM was used to define the effects of habitat, temperature, and their interaction on RMR, MMR, and AAS (Table 3). Temperature had a marginally significant effect on RMR (P = 0.053; Table 3), and no other significant terms were revealed. *Post hoc* ANOVAs and Tukey tests revealed a significant increase in reef fish RMR from 30 and 33 to 35°C (one-way ANOVA F = 6.972, P = 0.006; Tukey HSD 30–35 P = 0.008, 33–35 P = 0.019; Figure 3). In creek fish, RMR was significantly higher at 36°C than all other temperatures (one-way
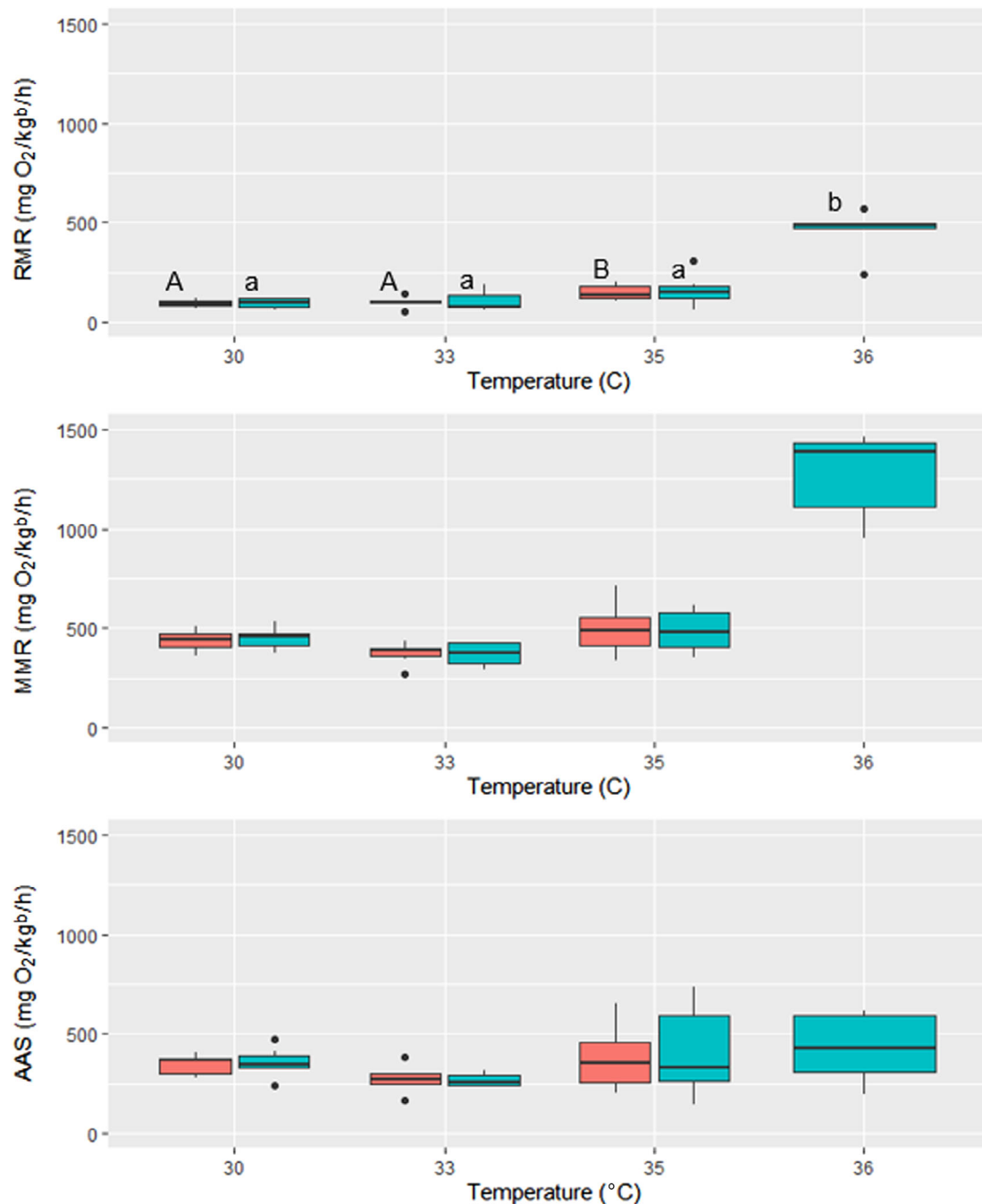
FIGURE 3 Mass-adjusted metabolic rates (mg O_2/kg^b/h) of creek- and reef-collected schoolmaster snapper across four acclimation temperature treatments. Top, mass-adjusted resting metabolic rate (RMR); middle, mass-adjusted maximum metabolic rate (MMR); bottom, mass-adjusted absolute aerobic scope (AAS = MMR – RMR). Different capitalized letters indicate significant differences between temperature treatments for reef fish (36°C was not included in the GLM because mortality precluded data collection for reef fish at that temperature). Different lower-case letters indicate significant differences between temperature treatments for creek fish. There were no significant differences in any of the metrics between habitats for any given temperature. 🟥, coral reef; 🟦, mangrove creek.

ANOVA $F = 39.71$, $P < 0.001$; Tukey HSD 30–36 $P < 0.001$, 33–36 $P < 0.001$, 35–36 $P < 0.001$; Figure 3). t-tests showed no significant differences across habitats for any of the metrics at any temperature, indicating that mass-corrected metabolic rates are relatively stable across habitats under similar temperatures. FAS (ratio of MMR to RMR) had a

nearly identical trend to AAS and therefore only AAS is presented and discussed, as per the recommendations in Halsey et al. (2018).

The U_{crit} of creek fish decreased with each increasing temperature treatment and was significantly lower at 36°C than at any other treatment (30 × 36°C, d.f. = 3, $P < 0.01$; 33 × 36°C, d.f. = 3, $P < 0.01$;

FIGURE 4   Absolute critical swimming speed for reef and creek-collected schoolmaster snapper across four temperature treatments. Significant differences within a collection habitat are denoted by different numbers of the same symbols. ─•─, reef; ─•─, creek.
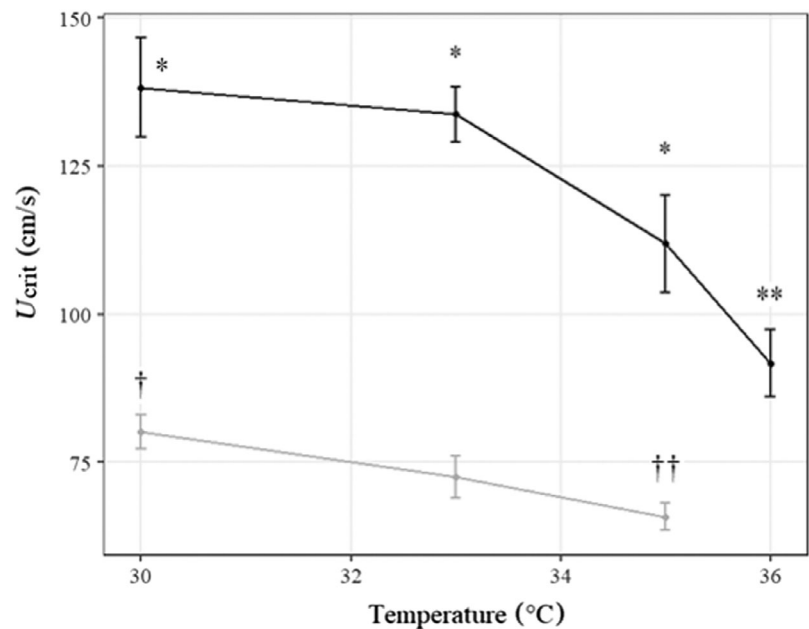
35 × 36°C, d.f. = 3, P = 0.04), falling 33.7% from 30 to 36°C (Figure 4). Although the U_{crit} of reef fish was not measured at 36°C due to mortality at that acclimation temperature, U_{crit} also declined with each higher temperature treatment, showing a significant decrease of 18% from 30 to 35°C (d.f. = 2, P < 0.01; Figure 4).

4 | DISCUSSION

Schoolmaster snapper, which occurs in two thermally distinct habitats, presents a unique opportunity to evaluate performance in response to thermal stress across a range of factors. Across the two groups of fish examined in this study, CT_{max} decreased as total length increased, but habitat was not a significant predictor. Additionally, critical swimming speed decreased with increasing temperatures. While RMR increased significantly at 35°C for reef fish and at 36°C for creek fish, MMR and AAS did not change across temperatures or habitats, indicating that the metabolic response to thermal stress is similar regardless of habitat. Together, these responses to acute (1–2 h in the CT_{max} trials) and longer (1 week acclimation prior to the metabolic rate measurements) temperature increases give insight into the susceptibility of the species in its different habitats.

Across the snapper that were sampled, CT_{max} decreased as size (TL) increased, and was higher in the creek fish than the reef fish. The CT_{max} findings suggest that creek-collected fish, that are likely juveniles, are more tolerant to thermal stressors than are reef-collected subadult or adult fish. These results were expected and as evidenced in a meta-analysis, larvae, juveniles and nonspawning adults across fish taxa are known to have a wider thermal tolerance than eggs and spawning adults (Dahlke et al., 2020). The reef fish used in this study were of reproductive size (>19 cm standard length [SL] per Starck II & Schroeder, 1971; Cocheret de la Moriniere et al., 2003) but they were not evaluated for maturity, so trends in CT_{max} cannot be solely

attributed to this reasoning. Additionally, the thermal profiles of the fish's habitats also corroborate this finding, as the higher maximum temperatures and more drastic fluctuations occurring in habitats such as tidal mangrove creeks typically harbour species or individuals with a higher thermal tolerance (Madeira et al., 2012). However, our findings are novel in that previous research, including a study by Ospina and Mora (2004), showed no significant changes in CT_{max} in relation to the body size of seven tropical reef fish. More importantly, the creek fish are operating within far slimmer thermal safety margins than the reef fish. The CT_{max} of the creek fish falls 1.8°C above the highest temperature recorded in that habitat, and it is unknown if this species would migrate out of nursery habitats to avoid detrimentally high temperatures. Alternatively, the CT_{max} of the reef fish was 7.8°C higher than the maximum temperature recorded at that site. A study by Madeira et al. (2012) compared the CT_{max} of many estuarine species and determined that those living in fluctuating environments operating close to their thermal limits were indeed the most vulnerable to thermal stress. If the thermal safety margins of these nearshore fish continue to narrow as sea surface temperature increases or if abnormal short heat waves occur more frequently, a combination of behavioural and physiological changes may need to occur to ensure the persistence of these populations in the face of acute heat events.

The measured metabolic responses (RMR, MMR, and AAS) of fish from the two habitats responded similarly to the different temperature treatments and interestingly, MMR and AAS did not change at all. A significant increase in RMR was seen in creek fish at 36°C, indicating an approach of a critical temperature in which fitness would decrease. While a significant increase in RMR was seen in reef fish at 35°C, no data were collected at 36°C due to high mortality during the week-long acclimation period, indicating that this critical temperature may have been reached by those fish, followed by physiological collapse. A stable AAS in both groups of fish as temperature increased was surprising as several previous studies on small reef fish have

found an overall decrease in aerobic scope in damselfish (*Dascyllus anuarus*, *Chromis atripectoralis* and *Acanthochromis polyacanthus*) and cardinalfish (*Ostorhinchus cyanosoma* and *O. doederleini*) when temperatures increased from 29 to 33°C (Nilsson et al., 2009). That study identified RMR as the parameter that caused the metabolic constraint, as it increased with temperature to narrow the aerobic window (Nilsson et al., 2009). Rummer et al. (2014) also exposed tropical reef fish to temperatures ranging from 29 to 34°C, and five of the six species tested exhibited either a peak in aerobic scope (denoting optimal temperature, T_{opt}) or the beginning of a plateau in aerobic scope at temperatures at or below 34°C, followed by a significant decrease in aerobic scope at increasing temperatures. In the context of the present study, aerobic performance did not vary across habitat following a longer (7 day) temperature challenge, but it did vary by fish size (a correlate of habitat) during an acute temperature challenge (1–2 h during the CT_{max} trials). By demonstrating that these different durations of heat exposure result in different responses, predictions can be made about how other ontogenetically separated species will respond to thermal stress.

Creek-collected *L. apodus* showed a decrease in U_{crit} as temperatures were increased, with 36°C being significantly lower than other treatments. Reef-collected U_{crit} responded in a similar pattern and significantly decreased as temperatures increased from 30 to 35°C. From the 30 to 35°C treatments, U_{crit} decreased by 16% in creek fish and by 18% in reef fish, showing a very similar response across the two groups of fish tested. Taken from the 30 to 36°C treatments, U_{crit} decreased by 34% in creek fish, which was an additional 18% decrease from the 35 to 36°C treatments. Above a species' T_{opt}, there is an inverse relationship between swimming speed and temperature (Johansen et al., 2014; Johansen & Jones, 2011). While the metabolic measurements in this study did not determine a peak in aerobic capacity for creek or reef fish (when AAS is highest, often denoted T_{opt}), it can be assumed that the optimal operating temperature for these snapper was lower than those temperatures tested due to the thermal profile of its range and collection site (mean temperature at reef site 28.7°C, mean temperature at creek site 29.1°C; Figure 1). The decrease in U_{crit} was therefore to be expected, and Johansen et al. (2014) also showed that in a similarly sized large tropical fish (common coral trout *Plectropomus leopardus*) spontaneous swimming speed decreased following a 3°C increase above control temperatures. Interestingly, the decrease in U_{crit} experienced by creek-collected snapper was nearly identical on a percentage basis to that of reef-collected individuals (16% and 18% decrease, respectively), a finding in line with the fact that the two groups of fish also had a similar response in metabolic rate across the treatment temperatures. There is a possibility for behavioural modification and spatial or temporal adaptation to elevated thermal conditions, as highlighted in several other studies (Baumann & Conover, 2011; Donelson et al., 2014; Johansen et al., 2014). However, it is unknown if these evolutionary responses will occur and allow tropical fish species to continue to persist. Recent studies have proposed that behavioural performance factors exceed physiological capabilities in terms of ecological importance (Castro-Santos, 2011), so critical swimming speed is therefore an applicable performance measure as it encompasses the ability for sustained locomotion and can be related to natural behaviours such as predator evasion and migration that would require such durational movement (Tierney, 2011). If energy is being reallocated away from swimming (as shown by the decrease in U_{crit} under thermal stress) and put towards physiological maintenance, behaviours (such as foraging, reproduction, etc.) that are vital to survival will be negatively affected. U_{crit} for both groups declined with increasing temperatures and could not be measured for reef fish above 35°C, and this essential performance factor (e.g., for escaping predators) is paramount in assessing how fish will react to thermal stress.

Species such as *L. apodus* that occupy multiple habitats based on life stage may be more susceptible to impending thermal stress due to the breadth of their life history. Seebacher and Franklin (2012) propose that the overall fitness of an organism is determined by the collective fitness, or lack thereof, at each ontogenetic stage. While having multiple ontogenetic stages inhabiting distinct areas would have been evolutionarily advantageous, thermal challenges to this and similar species could result in a greater opportunity for performance to be compromised. The substantial decrease in swimming capabilities quantified in this experiment brings to light the thermal constraints on the physiological performance of nearshore subtropical marine fishes under ephemeral thermal events and highlights the narrow thermal safety margin in nearshore juvenile habitats compared with reef-associated adults. Because the current study found substantial decreases in the critical swimming speed of *L. apodus*, future investigations should now be broadened to other economically, culturally, and ecologically important subtropical species that occupy habitats with similar fluctuating temperature regimes. Additional work on subtropical mesopredators across habitats and ontogeny is needed to determine their potential for acclimation or short-term genetic adaptation to environmental change to fully quantify the ecological consequences of warming on nearshore tropical communities. Lutjanids occupy both coral reef and mangrove ecosystems (Starck II & Schroeder, 1971), and if acute thermal events impact the juvenile stage that exists within a very narrow thermal safety margin, alterations to the structure of these marine communities may occur.

AUTHOR CONTRIBUTIONS

E.S., C.S., S.C., A.S. and Z.Z. contributed to study design and conception. E.S., A.S. and Z.Z. generated data. E.S., C.S., and B.T. analysed the data. E.S. prepared the manuscript. All authors contributed to editing the manuscript.

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