

RESEARCH ARTICLE

Developmental effects of heatwave conditions on the early life stages of a coral reef fish

Rachel K. Spinks*, Philip L. Munday and Jennifer M. Donelson

ABSTRACT

Marine heatwaves, which are increasing in frequency, duration and intensity owing to climate change, are an imminent threat to marine ecosystems. On coral reefs, heatwave conditions often coincide with periods of peak recruitment of juvenile fishes and exposure to elevated temperature may affect their development. However, whether differences in the duration of high temperature exposure have effects on individual performance is unknown. We exposed juvenile spiny damselfish, *Acanthochromis polyacanthus*, to increasing lengths of time (3, 7, 30 and 108 days post-hatching) of elevated temperature (+2°C). After 108 days, we measured escape performance at present-day control and elevated temperatures, standard length, mass and critical thermal maximum. Using a Bayesian approach, we show that 30 days or more exposure to +2°C leads to improved escape performance, irrespective of performance temperature, possibly owing to developmental effects of high temperature on muscle development and/or anaerobic metabolism. Continued exposure to elevated temperature for 108 days caused a reduction in body size compared with the control, but not in fish exposed to high temperature for 30 days or less. By contrast, exposure to elevated temperatures for any length of time had no effect on critical thermal maximum, which, combined with previous work, suggests a short-term physiological constraint of ~37°C in this species. Our study shows that extended exposure to increased temperature can affect the development of juvenile fishes, with potential immediate and future consequences for individual performance.

KEY WORDS: Developmental plasticity, Climate change, Exposure duration, Escape response, Body size, Bayesian analysis

INTRODUCTION

Marine heatwaves are damaging marine ecosystems worldwide, from mass bleaching of coral reefs (Hughes et al., 2017) to extensive kelp forest die-off (Wernberg et al., 2016). Defined as periods of abnormally high sea surface temperatures that persist for days to months, marine heatwaves have increased in frequency, duration and intensity over the past century, and can be linked to global warming (Frölicher et al., 2018; Oliver et al., 2018). Elevated sea temperature can have adverse impacts on marine life by increasing metabolic demands (Deutsch et al., 2015), affecting growth and survival (Pepin, 1991; Sheridan and Bickford, 2011) and modifying


behaviour (Nagelkerken and Munday, 2016). Furthermore, environmental extremes can have a greater impact on individuals and populations than gradual changes in average conditions (Vasseur et al., 2014). Importantly, marine heatwave conditions frequently coincide with periods of high juvenile abundance, and may therefore have fundamental effects on development and recruitment to the adult population.

Early life stages can be highly sensitive to environmental conditions, with potentially permanent consequences for the individual (West-Eberhard, 2003; Pörtner and Peck, 2010; Byrne, 2011). Exposure to altered conditions may induce phenotypic plasticity, which is the ability of a genotype to produce a range of phenotypes under different environmental conditions (Stearns, 1989). Whether environmental change results in phenotypic change can depend strongly on the timing of experience, with greater phenotypic plasticity often observed when change is experienced early in life (West-Eberhard, 2003). Known as developmental plasticity, phenotypic changes induced during early life conditions can have long-lasting effects (Angilletta, 2009). For example, cooler or warmer temperatures during embryonic development in zebrafish (*Danio rerio*) improved swimming performance and muscle phenotype of adults when exposed to the same temperatures of their embryonic period (Scott and Johnston, 2012). Beneficial phenotypic changes such as these can be adaptive, allowing organisms to adjust rapidly to altered environmental conditions if experienced during a sensitive period of development that is responsive to environmental factors (i.e. critical window; Burggren and Mueller, 2015). Conversely, plasticity can have energetic costs, and phenotypic changes in one trait may trade off with other traits (West-Eberhard, 2003). For example, increased temperature caused rapid growth and development of shark embryos, such that post-hatching body condition and survival were reduced (Rosa et al., 2014). Alternatively, stressful environmental conditions may simply have negative effects on phenotypic development, which was seen in newly hatched sea turtles with reduced ability to self-right, crawl and swim when developing at higher temperatures (Booth, 2017). While elevated water temperature during development can affect marine species, lasting effects will ultimately depend on the timing and duration of exposure to higher temperature and the traits involved.

As fishes are ectotherms with limited capacity for internal temperature regulation, environmental temperature directly influences the rate of cellular processes and physiological performance (Jobling, 1997). Consequently, higher water temperature will increase metabolic rate, influencing key biological processes that regulate life-history traits (Schulte, 2015). Tropical fishes can be affected by relatively small increases in temperature, with changes to aerobic scope (Nilsson et al., 2009), activity patterns (Johansen et al., 2014), escape responses (Allan et al., 2015), developmental rates (Green and Fisher, 2004) and growth (Munday et al., 2008). This suggests that they are currently living close to their

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Received 8 March 2019; Accepted 29 July 2019

thermal optima during summer and only have a safety margin of a few degrees Celsius before negative effects occur (Rummer et al., 2014; McLeod et al., 2015). The most thermally sensitive time for fishes is during reproduction and early development (Pankhurst and Munday, 2011; Pörtner and Peck, 2010). As coral reef fishes reproduce during spring and summer, this increases the probability that heatwave conditions will coincide with early developmental stages. This provides the opportunity for exposure during early life to produce lasting phenotypic changes to later life stages. Recent experiments have shown that continuous exposure to elevated water temperature throughout development can alter performance (Donelson, 2015). For example, exposure to 1.5–3°C above summer averages during early life can partially restore or even enhance aerobic scope of damselfish (Donelson et al., 2011; Donelson, 2015; Grenchik et al., 2013). In contrast, predominately negative developmental effects on body size, aerobic scope, escape performance and swimming ability were observed in juvenile wrasses exposed to 2°C above summer average (Motson and Donelson, 2017). These results suggest that exposure to higher temperature from early life may induce developmental changes to morphology or behaviour that, in turn, influence individual performance; however, all the relevant studies conducted to date have employed designs focused on testing the effect of long-term increases in average water temperature associated with global warming. Whether exposure to higher temperature for a restricted duration during early life, such as with heatwave conditions, induces lasting phenotypic change is currently unknown.

Here, we exposed juvenile spiny chromis damselfish, *Acanthochromis polyacanthus*, to elevated temperature (2°C above summer average temperature) for increasing lengths of time to test whether there were lasting effects on their individual performance. Specifically, we exposed damselfish to 3, 7, 30 or 108 days of elevated temperature from hatching to determine the influence on the resulting phenotypes compared with fish reared at present-day control temperature (for 108 days). The Great Barrier Reef recently experienced water temperatures of 1–2°C above current average summer temperatures, for days to weeks at a time (Fig. 1; Hughes et al., 2017). If global warming is constrained to a 1.5°C average increase above pre-industrial levels, marine heatwaves are expected to last on average 39 days and be up to 1.1°C hotter than in preindustrial times (Frölicher et al., 2018). However, if carbon

emissions are not curtailed, a business-as-usual scenario projects that marine heatwaves will likely last on average 112 days and be up to 2.5°C hotter than in preindustrial times (Frölicher et al., 2018). We therefore chose time frames and a temperature treatment that would sit between recent local observations and future global predictions. After the 108 days post-hatching (dph) rearing period, we measured a range of traits relevant to individual performance, including escape response (fast-starts), body size and critical thermal maximum, to determine whether increasing lengths of exposure to elevated temperature influenced the development and performance of these traits. Escape responses are predation avoidance techniques that entail high accelerations and a change in direction, aimed at displacing the prey away from the threat (Eaton, 1984). To establish whether developmental plasticity influenced the kinematics of an escape response, fish from all exposure duration treatments were tested at both control and elevated temperatures. Testing fish at both temperatures was completed so that effects owing to developmental conditions (i.e. plasticity) could be disentangled from the effect of the final temperature of each treatment at 108 days (Schulte et al., 2011). We also measured body size, which is a key fitness-related trait in juvenile fishes that links to competitive ability and predation risk (Sogard, 1997; Poulos and McCormick, 2015; Goatley and Bellwood, 2016). Reduced growth rates and smaller body size with increased warming is a commonly observed trend in fishes (Cheung et al., 2013; Munday et al., 2008). Lastly, we measured critical thermal maximum (CT_{max}) as it defines the upper lethal limits at which an animal's locomotor activity becomes disorganised and can no longer escape from conditions that will lead to death (Cowles and Bogert, 1944). While some studies have shown that CT_{max} of adult reef fishes can increase following exposure to elevated temperatures (Barker et al., 2018; Eme and Bennett, 2009; Habary et al., 2016), other studies have found no change in CT_{max} (e.g. Donelson, 2015). Whether experiences to elevated temperature for a restricted duration during early life has a persistent effect on CT_{max} is unknown.

MATERIALS AND METHODS

Study species

Acanthochromis polyacanthus (Bleeker 1855) is a widespread Indo-Pacific coral reef damselfish that forms monogamous pairs (Miller-Sims et al., 2008; Robertson, 1973). They breed during the

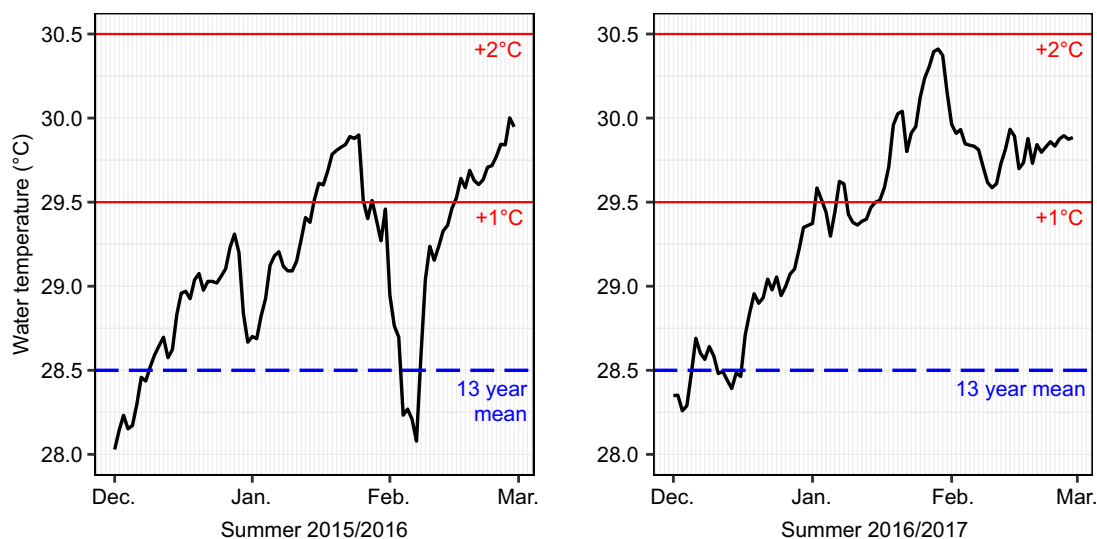


Fig. 1. Daily mean sea temperatures during marine heatwave events. Recorded during the 2015/2016 and 2016/2017 austral summers at 6 m depth on Orpheus Island reef, central Great Barrier Reef (AIMS, 2017). The blue dashed lines show the summer average from 2002 to 2015 (AIMS, 2016).

warmer months, most often between October and February (Robertson, 1973). They lay clutches of 250–500 eggs, adhered to the substrate, with an average embryonic period of 9 days at 28.5°C (Kavanagh, 2000; R. K. Spinks, unpublished data). This species lacks a pelagic larval stage (Robertson, 1973) and juveniles remain with their parents for a few months after hatching (Kavanagh, 2000; Robertson, 1973).

Broodstock

Adult *A. polyacanthus* were collected from Bramble Reef (18°22'S, 146°40'E) on the central Great Barrier Reef and Holmes Reef (16°28'S, 147°52'E) in the Coral Sea in July 2015 and 2016, respectively. Fish were transported to the Marine and Aquaculture Research Facility at James Cook University, Townsville, Australia, and housed in breeding pairs within 42 litre tanks, each with half a terracotta pot as a shelter and spawning site. Tanks were supplied with a continuous flow of seawater from a 25,000 litre recirculating system with precise temperature control (6×2 kW Control Distributions custom-built heaters, Carlton, NSW, Australia; 18 kW Solarwise chiller EXC341RC, Kingston, QLD, Australia; PR Electronics temperature transmitter 5333A, ±0.1°C, Rønde, Denmark). Water quality was maintained with mechanical, biological and ultraviolet filtration, and protein skimming. Pairs were kept at seasonally cycling, present-day sea temperature for the region where fish were collected based on temperature loggers around Orpheus Island from 2002 to 2015 at 0.2–14.6 m depth (Fig. S1; AIMS, 2016). Light levels followed the natural seasonal cycle. Adult fish were fed *ad libitum* on commercial fish pellets (NRD G12, INVE Aquaculture, Salt Lake City, UT, USA) at least once a day. When summer average water temperature (28.5°C) was reached in November 2016, aquaria were checked every morning for the presence of newly laid egg clutches. The first clutches from four pairs laid in December 2016 and January 2017 were used in this experiment. All clutches remained with the parents during embryonic development, allowing them to provide nest care as occurs in the wild. Within 3 h of hatching, the offspring were removed from the parents' tank and transferred to experimental treatments.

Experimental design

Juveniles were reared for 108 dph at the average summer sea temperature for the central Great Barrier Reef (present-day control mean: 28.5°C) and in four treatments where they were exposed to a higher temperature (+2°C mean: 30.5°C) for 3, 7 or 30 dph, or for the entire 108 days of the experiment. After exposure to the elevated temperature for 3, 7 or 30 dph, juveniles were returned to the control temperature until performance testing. For each of the four clutches, newly hatched juveniles were randomly allocated to three replicate tanks at each treatment level (i.e. 15 tanks total per clutch), with 10 fish per tank. To represent natural reef conditions, a diurnal temperature cycle (±0.6°C) that rose during the day and cooled at night, was employed for the present-day control and elevated temperatures. Newly hatched juveniles were transferred to experimental tanks in a 2 litre tub that was then half-submerged in the tank with a partial water exchange over 3 h to slowly equilibrate temperature. This protocol was also employed for the temperature shifts at 3, 7 and 30 dph. To prevent handling bias, the fish reared for 108 dph at the present-day control and the elevated treatment were likewise shifted to new aquaria at 30 dph. No mortalities occurred during these transitions. In total, only 0.5% mortality occurred during the 108-day rearing period. Illumination was kept at the average summer photoperiod (12 h:12 h light:dark) throughout the experiment. Feeding rates were the same for all treatments. Juveniles

were fed approximately 10 mg (dried cyst mass) per individual of live *Artemia nauplii* the first 3 days, then weaned to 2 mg per individual of 200–400 µm size NRD pellets and finally increased to 3 mg per individual of 500–800 µm size NRD pellets (INVE Aquaculture) at 30 dph. This is considered a high feeding level (at an average of 1–2% of their body mass) for captive *A. polyacanthus* on an energy-rich formulated diet (Donelson et al., 2010). Prior to trials, fish were starved for 12 h. This research was conducted under James Cook University's ethics approval A2315.

Escape response

To determine the influence of thermal exposure duration on escape performance, we measured six escape response traits at the end of the experiment (between 109 and 121 dph) in fish that had been exposed to an average of +2°C for 0, 3, 7, 30 and 108 dph. For each treatment level, we measured the escape responses at the mean present-day control (28.5°C) and mean elevated temperature (30.5°C). Fish were randomly allocated (50/50) to these performance temperatures a minimum of 7 days prior to trials to prevent an acute stress reaction. All fish were shifted, following the same temperature transition protocol described above, even if they stayed in the same temperature. Trials were conducted between 09:00 and 18:00 h, over 7 days. To prevent any time or day bias, testing of fish was random across treatments and tank replicates. Using a standard protocol by Allan et al. (2014), fish were introduced into a circular arena (Ø 32 cm, height 9 cm) via a water-filled container and allowed 2 min to acclimate. The arena sat inside an opaque plastic tank (Ø 64 cm, 348 litres) with a transparent acrylic bottom to allow responses to be filmed from below via a high-speed camera (480 frames s⁻¹, Casio Exilim EX-ZR2000, Tokyo, Japan) pointed at a mirror on a 45 deg angle. A 5 cm line drawn on the bottom of the tank enabled calibration for video analysis. The top and underside of the tank were covered to prevent disturbance to the fish. Illumination of the arena was via LED strips (Arlec cool white 1000 lm, Blackburn North, VIC, Australia) wrapped around the outside of the tank. The arena was filled to 4 cm to minimise vertical movement of the fish in the water column. A 25 W glass heater (Kong's Aqua one 11301, Ingelburn, NSW, Australia) with a digital thermostat (Tic-17RGTi, Full Gauge Controls, Canoas, Brazil) that maintained the set-point temperature within ±0.1°C was immersed between the arena and tank wall, along with four air stones for oxygenation.

Fish were startled once only by the release of a conical, black-tipped magnet from an electromagnetic device. The magnet was secured to the electromagnet device via fishing line so that the tapered tip just touched the water surface. To prevent a premature response associated with visual stimulation, the magnet fell through a PVC pipe (Ø 4 cm) suspended 1 cm above the water surface. Fish were startled at least one body length away from the arena's wall to reduce edge effects on escape responses (Eaton and Emberley, 1991). When the stimulus first hit the water surface, we measured the direction the fish were facing from the stimulus and the distance between the fish and the stimulus to determine whether there were any differences between treatments and performance temperatures. After 10 min, if the fish did not leave the arena's wall, no startle attempt was made and the trial ended. After each trial, the arena was flushed with new water, and after five trials the whole tank was drained and refilled.

The following escape response traits were measured: (1) response latency – defined as the time (ms) between the onset of the stimulus hitting the water's surface and the first detectable movement of the head; (2) response probability – classified as a C-start escape

response or non-C-start response in reaction to the stimulus [a C-start escape response begins at the first detectable movement of the head, the fish makes a C-shape rotation and ends when the body straightens out (akin to stages 1 and 2 defined by Domenici and Blake, 1997)]; (3) escape maximum speed – defined as the maximum speed (m s^{-1}) reached at any point during a C-start escape response; (4) escape mean speed – defined as the average speed (m s^{-1}) during a C-start escape response within a given time interval of 20 ms (this corresponds to the average C-start escape response for all fish); (5) escape distance – defined as the total distance (mm) covered during a C-start escape response within a given time interval of 20 ms; and (6) escape direction – defined as the direction (deg) after the C-start escape rotation, relative to the stimulus.

Larger fish are known to perform faster escape responses and travel further; therefore, fish standard length was included as a covariate in escape speed and distance models (Domenici and Blake, 1997). Additionally, initial orientation of the fish from the stimulus is known to influence escape direction, hence orientation on stimulus impact was included as a covariate in the escape direction model (Domenici and Blake, 1993). Videos were analysed blind using ImageJ software v. 1.50i (Schneider et al., 2012) with the manual tracking plugin. We standardised tracking from the head of the fish (~10% of the standard length) as it was the most reliable area to track.

Body size

To determine the influence of thermal exposure duration on body size, we measured standard length (± 0.02 mm) and wet mass (± 0.001 g) of 589 fish immediately after escape response and CT_{max} trials. Because sex can often influence body size (Parker, 1992), we included it as a covariate when modelling standard length and mass. After size measurements, fish were sexed under the microscope via external examination of the urogenital papilla.

Critical thermal maximum

To investigate the influence of thermal exposure duration on CT_{max} , a dynamic method or ramping assay was used. The rate of increase applied was 0.5°C every 30 min ($0.017^{\circ}\text{C min}^{-1}$) until the fish lost equilibrium for at least 5 s. Loss of equilibrium was determined by the inability of the fish to right itself. This rate of warming has been used in other CT_{max} studies on *A. polyacanthus* (Clark et al., 2017; Rodgers et al., 2018). The CT_{max} was measured for each family between 109 and 117 dph, over three separate days. A total of 24 fish at each treatment level were tested. These 24 fish consisted of six fish from each of the four families, of which two fish came from each of the three tank replicates in each treatment by family combination. Fish were introduced at their final rearing temperature (i.e. 28.5°C for 0, 3, 7 and 30 dph and 30.5°C for 108 dph exposure duration treatments) into one of six mesh chambers (\varnothing 15 cm, height 20 cm) inside a 150 litre opaque plastic aquarium. Two fish were placed in each chamber to reduce stress because *A. polyacanthus* is a social species and the fish were raised in groups. For each trial, fish were randomly selected across treatments and tank replicates. Inside the aquarium were two air stones for oxygenation of water and a 1 kW heater (Omega, Norwalk, CT, USA) with a digital thermostat (Tic-17RGTi, Full Gauge Controls) that maintained the set-point temperature within $\pm 0.1^{\circ}\text{C}$. Temperature was also manually measured every 30 min with a digital thermometer ($\pm 0.1^{\circ}\text{C}$, C26, Comark Instruments, Norwich, Norfolk, UK) to confirm it matched the thermostat readings. Immediately after the trial, fish were euthanised by an overdose of clove oil.

Statistical analyses

We chose to analyse our data in a Bayesian framework because it allows exploration of complex random-effects structure, handles unbalanced designs with ease, has more appropriate estimates of uncertainty, and allows integration of prior information (Kruschke, 2015). All analyses were performed in R v. 3.5.1 (<https://www.r-project.org/>; see Script 1), with figures created in the ggplot2 package (Wickham, 2016).

Hierarchical mixed models

We used the rstanarm package v. 2.17.4 (<https://mc-stan.org>) to implement Bayesian hierarchical mixed models. All models included the ‘fixed’ effect of exposure duration treatment (0, 3, 7, 30 and 108 dph at $+2^{\circ}\text{C}$). Escape performance models also included the fixed effect of performance temperature (28.5°C , 30.5°C) and, when appropriate, the covariates standard length and escape duration (Table 1). Body size models included sex as a covariate and CT_{max} models included standard length (Table 1). Continuous covariates were centred to improve model optimisation and scaled for comparison purposes. All relevant interactions were explored. The ‘random’ effects structure was defined by tank nested within family for all models, with CT_{max} models additionally including trial date as a random effect (Table 1). This structure was necessary to control for non-independence of fish raised in the same tank, fish from the same family and fish in the same CT_{max} trial, and to account for the hierarchical experimental design (Harrison et al., 2018). A random-intercept model was used in all circumstances except for standard length, mass and CT_{max} (Table 1). In these latter three, a random-slope random-intercept model fitted best (visually and via model selection) because the slopes differed between the dependent variable (e.g. mass) and the treatments (Table 1). Gaussian distributions with an identity link were employed in the following models: escape mean speed, escape maximum speed, escape distance, distance from stimulus, standard length, mass and CT_{max} (Table 1). To improve the model fit of response latency, an inverse Gaussian distribution with an identity link was used. To model the binary dependent variables, response probability and sex ratio, we used a binomial distribution with a logit link.

Bayesian models incorporate prior knowledge, which can be: (1) informative, if specific knowledge exists, (2) weakly informative, if general knowledge exists, or (3) non-informative, if no knowledge exists. We specified an informative normal intercept prior mean for standard length, mass and CT_{max} (Table 2). The informative priors were selected because Rodgers et al. (2017) found that *A. polyacanthus* exposed to present-day sea temperatures for 90 dph were an average standard length of 33.99 mm and wet mass of 1.21 g. Additionally, the CT_{max} of two lower latitude populations of *A. polyacanthus* were defined at an average of 37.07°C (Rodgers et al., 2018) and 36.58°C (Clark et al., 2017). In all other instances, we specified weakly informative normal intercept and normal slope and half Cauchy error standard deviation priors (Table 2). A half Cauchy distribution for the error standard deviation prior was selected as it is ideal with weakly informative priors and hierarchical models (Gelman, 2006). The prior on the covariance matrix for all models was specified as regularization=1, concentration=1, shape=1, scale=1, which implies a uniform prior over all correlation matrices and simplex vectors with a unit-exponential distribution, which is a robust default prior in most hierarchical designs (Muth et al., 2018). Visual posterior checks confirmed that priors never heavily influenced the posteriors. Models used Hamiltonian Monte Carlo, which is a Markov chain Monte Carlo (MCMC) method. Models were run with three chains using the no-U-turn sampler

Table 1. Final models fitted

Dependent variable	Fixed effects	Random effects	Distribution, link function
Response latency	Treatment+Performance temp.	Random intercept: Tank nested in Family	Inverse Gaussian, identity
Response probability	Treatment+Performance temp.	Random intercept: Tank nested in Family	Binomial, logit
Escape mean speed	Treatment+Performance temp.+Standard length+Escape duration	Random intercept: Tank nested in Family	Gaussian, identity
Escape maximum speed	Treatment+Performance temp.+Standard length	Random intercept: Tank nested in Family	Gaussian, identity
Escape distance	Treatment+Performance temp.+Standard length+Escape duration	Random intercept: Tank nested in Family	Gaussian, identity
Escape direction	Treatment+Performance temp.+Orientation on stimulus impact	NA	Circular projected Gaussian
Orientation on stimulus impact	Treatment+Performance temp.	NA	Circular projected Gaussian
Distance from stimulus	Treatment+Performance temp.	Random intercept: Tank nested in Family	Gaussian, identity
Standard length	Treatment+Sex	Random slope: Treatment	Gaussian, identity
Mass	Treatment+Sex	Random intercept: Tank nested in Family Random slope: Treatment	Gaussian, identity
Sex ratio	Treatment	Random intercept: Tank nested in Family	Binomial, logit
Critical thermal maximum	Treatment×Standard length	Random intercept: Tank nested in Family Random slope: Treatment Random intercept: Tank nested in Family Trial date	Gaussian, identity

Orientation on stimulus impact was transformed to cosine and sine components to maintain the circular characteristics when used as a covariate. NA, not applicable.

(NUTS) for 5000 iterations, with the first 1000 samples discarded. Every second sample was thinned. Thus, posterior distributions derived from each Markov chain comprised 2000 samples.

Model validation and selection

Models were confirmed to be well mixed and converge on a stable posterior via visual inspection of the trace plots. In some models, better mixing of chains was encouraged by reducing the step size and thus controlling the resolution of the sampler. Densities of all three chains closely agreed and were normally distributed. \hat{R} values were below 1.05 and effective sample sizes neared 100%. Posterior sample distributions closely reflected the actual distribution of the data. Visual inspection confirmed residuals were homogeneous and, when relevant, illustrated linearity. We compared models for predictive accuracy using Pareto smoothed importance sampling leave-one-out cross-validation (PSIS-LOOCV), implemented using loo package v. 2.0.0 (Vehtari et al., 2017). This is performed by estimating the difference in the models' expected log predicted density (ELPD) and generating a LOO information criterion (LOOIC), along with its uncertainty. LOOIC is similar to Akaike's information criterion (Akaike, 1973), but takes priors into account, and makes no distributional assumption about the posterior (Vehtari et al., 2017). Models with lower LOOIC values

are expected to have higher predictive accuracy. Final models were selected for inference based on LOOIC values and parsimony (Bates et al., 2015 preprint). General conclusions were identical for models with similar LOOIC values.

Circular models

Escape direction and orientation on stimulus impact are periodic dependent variables requiring circular analysis methods. We used the `bpnreg` package v. 1.0.0 (<https://CRAN.R-project.org/package=bpnreg>) to implement a Bayesian embedding approach to circular regression with a projected Gaussian distribution. Both models included exposure duration treatment and performance temperature as fixed effects, while the escape direction model also included orientation on stimulus impact as a covariate, which was transformed to sine and cosine components to maintain its circular characteristics (Pewsey et al., 2013) (Table 1). We were unable to run mixed effects models owing to the unbalanced design of our random effects, with no known alternative software. Directional variables were converted to radians prior to analysis and then transformed to circular coefficients as per Cremers et al. (2018) and Cremers and Klugkist (2018). The default weakly informative priors were used, which specified a normal prior of 0 for the regression coefficients and intercept for each of the two

Table 2. Priors used in the hierarchical mixed models

Model	Intercept	Slope	Error standard deviation
Response latency	Normal (0, 100 ms)	Normal (0, 50 ms)	Cauchy (0, 25 ms)
Response probability	Normal (0, 10)	Normal (0, 2.5)	NA
Escape mean speed	Normal (0, 2.72 m s ⁻¹)	Normal (0, 0.68 m s ⁻¹)	Cauchy (0, 1.36 m s ⁻¹)
Escape max. speed	Normal (0, 5.65 m s ⁻¹)	Normal (0, 1.41 m s ⁻¹)	Cauchy (0, 2.82 m s ⁻¹)
Escape distance	Normal (0, 95.34 mm)	Normal (0, 23.83 mm)	Cauchy (0, 47.67 mm)
Distance from stimulus	Normal (0, 214.32 mm)	Normal (0, 53.58 mm)	Cauchy (0, 107.16 mm)
Standard length	Normal (34, 26.11 mm)	Normal (0, 6.53 mm)	Cauchy (0, 13.06 mm)
Mass	Normal (1.2, 4.19 g)	Normal (0, 1.05 g)	Cauchy (0, 2.09 g)
Sex ratio	Normal (0, 10)	Normal (0, 2.5)	NA
Critical thermal max.	Normal (37, 0.91°C)	Normal (0, 0.46°C)	Cauchy (0, 0.91°C)

The prior distribution is provided along with the mean and standard deviation in brackets. The majority of the standard deviations (also known as scales) were internally specified by multiplication of the standard deviation of the dependent variable via the `rstanarm` package. NA, not applicable.

components, and a prior precision matrix with diagonal values equal to 0.001 (<https://CRAN.R-project.org/package=bpnreg>; Cremers et al., 2018). Models used the same MCMC method, NUTS sampler, and number of chains, iterations and warm up as above. Model validation was also as previously mentioned; however, model selection was via the Bayesian Watanabe–Akaike information criterion (WAIC; Watanabe, 2010), akin to LOOIC.

Estimates of uncertainty

With Bayesian estimates of uncertainty (here we used the highest posterior density uncertainty interval), we can state that we are sure that the true value of the response lies within this interval. Contrast this with confidence intervals used in a Frequentist framework, with which we can say the response may fall within this interval, 95 out of 100 times if the confidence level is set to 95%. In this study, strong evidence for an effect (i.e. statistical ‘significance’) is defined when the 95% uncertainty interval (UI) does not intersect with zero. Moderate evidence for an effect is inferred when 85% of the UI lies to one side of zero.

RESULTS

Escape response

Response latency demonstrated no evidence (i.e. the $\geq 85\%$ UI intersected with zero) of a difference between the exposure duration treatments or between performance temperatures (Fig. 2A). All but one fish, which was facing 180 deg away from the stimulus upon impact, responded to the stimulus. The majority ($\sim 80\%$) of reactions were C-start escape responses. Non-C-start responses included moving slowing backwards or even towards the stimulus in a few instances. However, there was no evidence of a difference in the probability of producing a non-C-start response between the exposure duration treatments and control (Fig. 2B). Performance temperature also did not influence the probability of producing a non-C-start response (Fig. 2B).

Exposure to $+2^\circ\text{C}$ for 30 and 108 dph resulted in moderate evidence towards an increase in escape mean speed (i.e. the 85% UI did not intersect with zero: 30 dph, 0.026 to 0.189 m s^{-1} ; 108 dph, 0.016 to 0.183 m s^{-1}), with fish escaping on average 9% (30 dph) and 8% (108 dph) faster than control fish (Fig. 2C). Performance temperature did not influence the escape mean speed of juveniles (Fig. 2C). There was strong evidence (i.e. the 95% UI did not intersect with zero) that longer fish escaped faster, irrespective of thermal exposure duration (Fig. S2). The fixed effects of the escape mean speed model (treatment, performance temperature, standard length and C-start duration) explained 12% variability (marginal r^2), whilst the whole model including the random effects (tank nested in family) explained 14% variability (conditional r^2) of escape mean speed. Escape maximum speed, in contrast, showed no evidence of a difference between the exposure duration treatments and 30.5°C performance temperature compared with the control (Fig. 2D). Escape maximum speed also showed no influence of fish standard length (Fig. S2).

Fish exposed for 30 and 108 dph to elevated temperatures showed moderate evidence of travelling further during an escape response (85% UI: 30 dph, 0.518 to 4.18 mm; 108 dph, 0.012 to 3.89 mm), with fish travelling on average 10% (30 dph) and 8% (108 dph) further than control fish (Fig. 2E). There was strong evidence that longer fish moved further, irrespective of thermal exposure duration (Fig. S2). The model explained 61% (marginal r^2) and 62% (conditional r^2) variability of escape distance. Fish exposed for 108 dph to elevated temperatures showed strong evidence of a change in escape direction, which was on average 34 deg clockwise

from control fish, albeit all fish escaped in a direction away from the stimulus (Fig. 2F; Table S1). There was no evidence that performance temperature had an effect on escape direction (Fig. 2F; Table S1).

The orientation fish were facing on stimulus impact demonstrated no evidence of a difference in exposure duration treatments compared with control fish (Fig. S3A). There was strong evidence for a ~ 20 deg clockwise change in orientation on stimulus impact in fish performing an escape at 30.5°C compared with 28.5°C (control), but the orientation was still towards the stimulus (Fig. S3A). Escape direction model fits were greatly improved when adding orientation on stimulus impact as a covariate. Finally, fish exposed for 30 dph showed strong evidence of being closer to the stimulus on impact compared with control fish (median difference: -9.14 mm; 95% UI: -16.8 to -1.97 mm; Fig. S3B), yet treatment and performance temperature explained only 4% variability (marginal r^2) of this distance. Escape response model fits were not improved when adding distance from stimulus as a covariate.

Body size

Fish with 3, 7 and 30 days’ exposure post-hatching to elevated temperature showed no strong evidence of a change in standard length or mass compared with control fish (Fig. 3). There was moderate evidence for a decline in standard length for fish exposed for 7 dph (85% UI: -1.42 to -0.18 mm), but the effect was small, with an average decline of 2%. By contrast, fish experiencing the entire 108 dph at elevated temperatures displayed strong evidence for a decline in body size (95% UI: standard length, -3.95 to -1.42 mm; mass, -0.509 to -0.111 g), with fish on average 7% shorter and 16% lighter than control fish (Fig. 3). In addition, there was moderate evidence for sex differences (85% UI: standard length, -0.58 to -0.05 mm; mass -0.105 to -0.015 g), with males on average 1% shorter and 3% lighter than females (Fig. 3). The models explained 14% (marginal r^2) and 27% (conditional r^2) variability of standard length and 10% (marginal r^2) and 23% (conditional r^2) variability of mass. There was no evidence for a difference in sex ratios between the control and exposure duration treatments (Fig. S4).

Critical thermal maximum

Fish exposed to increasing lengths of warming showed no evidence of a change in CT_{max} compared with control fish (Fig. 4). Strong evidence demonstrated longer fish withstand a higher CT_{max} ; however, there was an interaction because fish in the 3 dph exposure duration treatment exhibited the opposite trend (Fig. S5). The model explained 21% (marginal r^2) and 61% (conditional r^2) variability of CT_{max} . Finally, there was no evidence that trial starting temperature had an influence on CT_{max} outcomes.

DISCUSSION

Our results show that extended exposure to heatwave conditions, early in life, can affect ecologically important traits in juvenile reef fish. Exposure to $+2^\circ\text{C}$ conditions for 30 or 108 dph enhanced the mean escape speed and escape distance. Fish continuously exposed to increased temperatures (108 dph) also experienced a change in escape direction. Shorter exposure durations of 3 and 7 dph did not result in changes to escape performance, potentially indicating that the length of exposure was not sufficient to cause phenotypic change. Increases in escape speed and distance away from a potential predator would likely be beneficial in a natural reef setting. Fish continuously exposed to elevated temperatures from hatching (108 dph) were substantially smaller, illustrating the potential

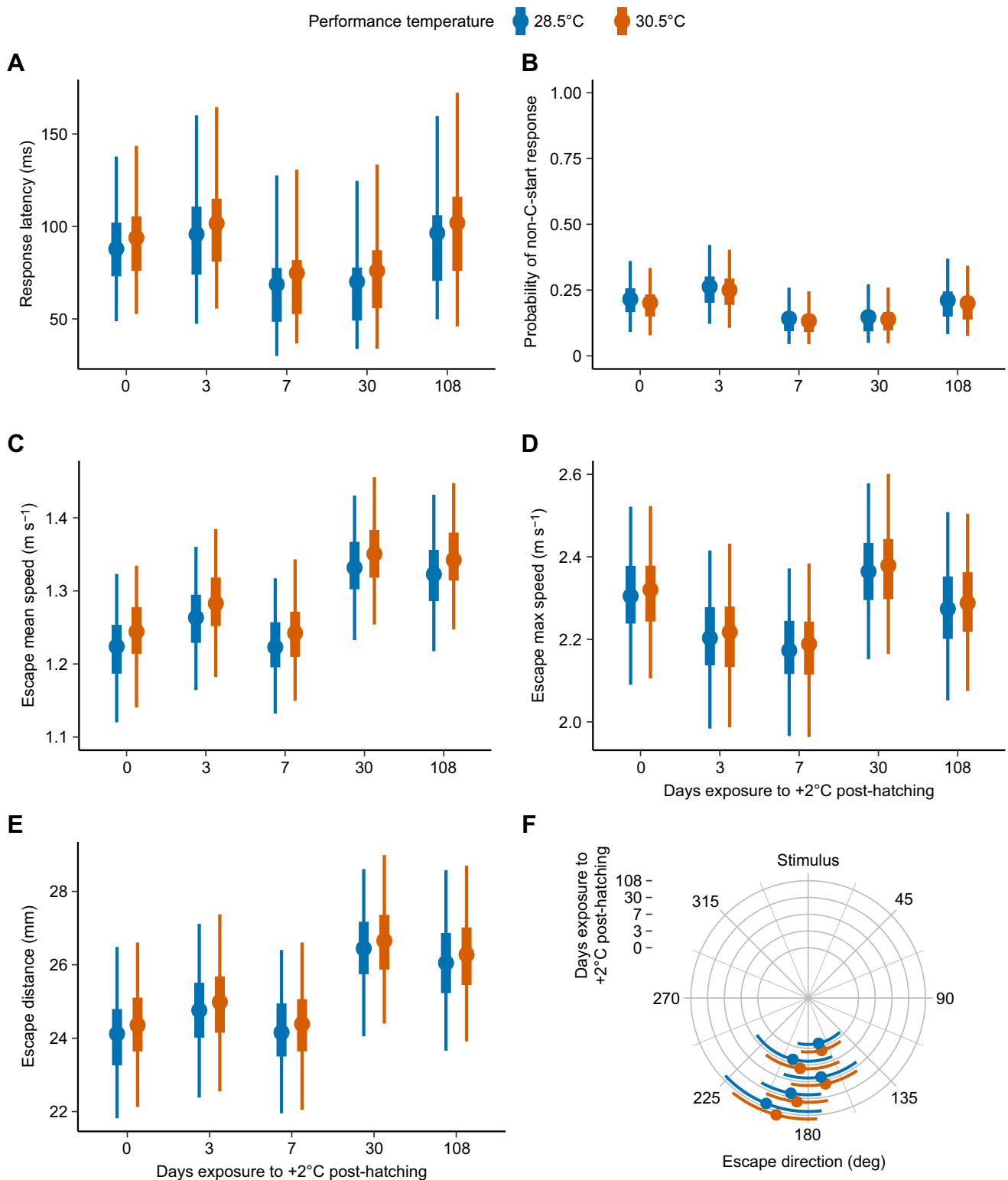


Fig. 2. Escape performance in the damselfish *Acanthochromis polyacanthus*. Bayesian posterior median values (circles), 95% highest posterior density uncertainty intervals (thin lines) and 50% uncertainty intervals (thick lines) of (A) response latency, (B) probability of non-C-start response, (C) escape mean speed, (D) escape maximum speed and (E) escape distance. Plots C–E are held at the average standard length (36.10 mm) of fish tested. (F) Bayesian posterior mean values (circles) and 95% highest posterior density uncertainty intervals (lines) of escape direction. Numbers on the left correspond (from top to bottom) to outer to inner circles of the chart. Moderate evidence supported the 30 and 108 dph treatments having a faster escape mean speed and further escape distance in both performance temperatures compared with the control (0 dph). Strong evidence supported the 108 dph treatment turning further clockwise in both performance temperatures compared with the control (0 dph). (A,B) $N=59$ (0 dph), 59 (3 dph), 60 (7 dph), 57 (30 dph), 54 (108 dph); (C–F) $N=46$ (0 dph), 43 (3 dph), 51 (7 dph), 47 (30 dph), 42 (108 dph).

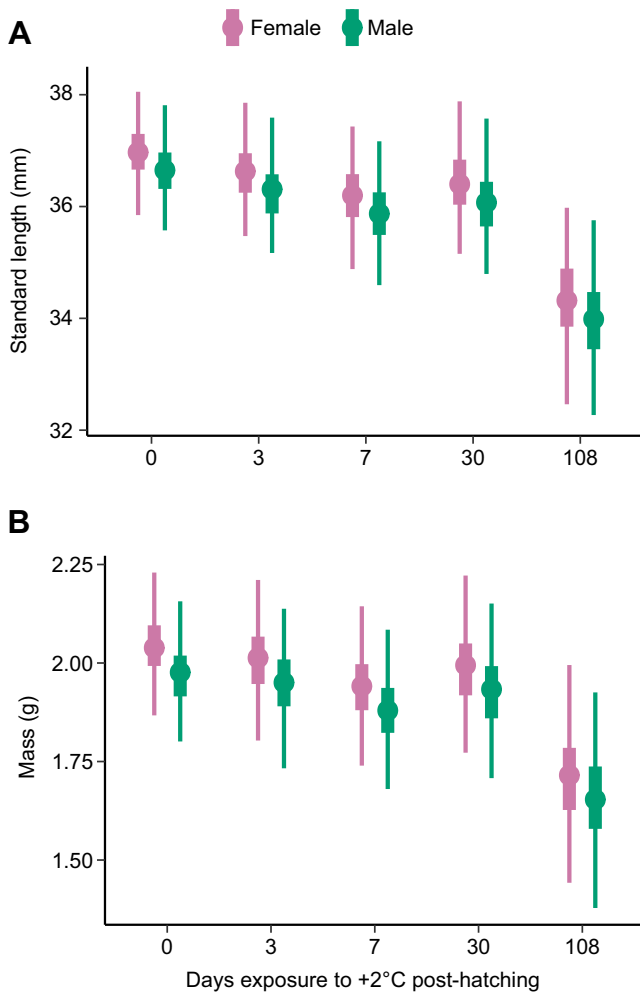


Fig. 3. Body size in *A. polyacanthus*. Bayesian posterior median values (circles) with highest posterior density 95% uncertainty intervals (thin lines) and 50% uncertainty intervals (thick lines) of fish (A) standard length and (B) wet mass. Strong evidence supported the 108 dph treatment being shorter and lighter compared with the control (0 dph). Moderate evidence supported males being shorter and lighter in all groups. $N=114$ (0 dph), 120 (3 dph), 120 (7 dph), 116 (30 dph), 119 (108 dph).

energetic cost of ongoing exposure to warming. By contrast, fish exposed for 3, 7 and 30 dph to increased temperatures did not exhibit considerable reductions in body size. This may be because the length of exposure was insufficient to have an effect on growth, or alternatively could be due to compensatory growth following an initial period of reduced growth during high temperature exposure (Metcalf and Monaghan, 2001). No effect of thermal exposure duration was observed for CT_{max} , and combined with previous work in *A. polyacanthus* (Clark et al., 2017; Rodgers et al., 2018; Zarco-Perelló et al. 2012), this suggests a short-term physiological constraint of $\sim 37^{\circ}\text{C}$ in this species.

Developmental plasticity allowed fish exposed for 30 and 108 dph to simulated heatwave conditions to swim faster and further during an escape compared with fish reared at present-day control temperatures. Enhanced mean escape speed and distance in 30 and 108 dph treatment fish was observed in both of the performance temperatures, demonstrating that this was a developmental effect rather than an effect of water temperature at the time of testing. This potentially indicates that the altered phenotypes were fixed in place during a critical window after 8 dph,

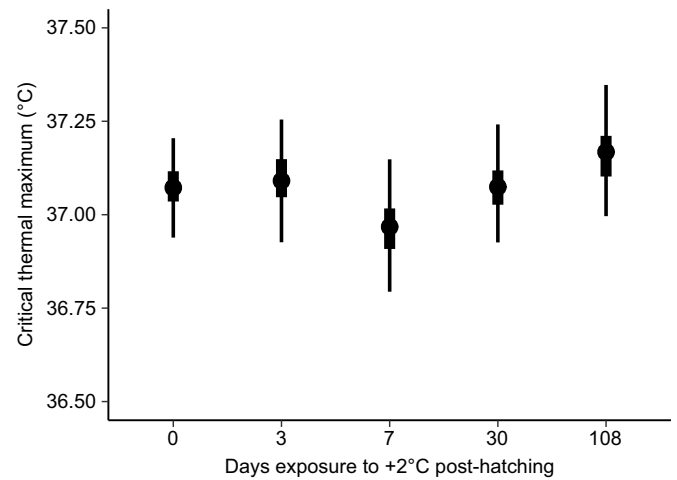


Fig. 4. Critical thermal maximum in *A. polyacanthus*. Bayesian posterior median values (circles) with 95% highest posterior density uncertainty intervals (thin lines) and 50% uncertainty intervals (thick lines) of the critical thermal maximum at the average standard length (35.82 mm) of fish tested. There was no evidence of a difference between the treatments. $N=24$ fish per treatment.

but before 30 dph. Jarrold and Munday's (2018) study supports this idea, as they found enhancements in escape speed, distance and turning rate in *A. polyacanthus* reared at $+2^{\circ}\text{C}$ for 28 dph. The phenotypic change observed in 30 and 108 dph is also likely related to the length of exposure (Schulte et al., 2011), with exposure greater than 7 dph required to induce phenotypic change. Because phenotypic change is energetically costly, responding to incorrect cues would be maladaptive, thus it is likely that a certain duration of cue exposure would be required before a permanent phenotypic change is induced (Angilletta, 2009). Determining the interplay between timing and length of exposure would require additional investigation; however, combining the present results with previous research on the thermal sensitivity of *A. polyacanthus* during early life suggests that juveniles remain sensitive to warming between 30 and 60 dph (Donelson et al., 2011; Rodgers et al., 2017). This suggests that the duration of exposure may be more critical to inducing phenotypic change observed and juveniles could be affected when they experience heatwaves within the first months of life.

Increases in speed and distance travelled during an escape response would likely result in higher chances of survival from a predatory attempt. For example, Walker et al. (2005) showed that when guppies (*Poecilia reticulata*) increased escape speed and distance travelled, they had higher odds of surviving a predation strike by a natural predator. Moreover, certain vertebral phenotypes of threespine sticklebacks (*Gasterosteus aculeatus*) produced faster escape speeds and were more likely to survive predator attacks (Swain, 1992a,b). Increased speed and distance travelled during the escape response are likely due to differences in muscle development and/or anaerobic metabolism (Domenici et al., 2008; Domenici and Blake, 1997). For example, improvement in fast-start locomotor performance of short-horned sculpin (*Myoxocephalus scorpio*) exposed for a minimum of 6 weeks to elevated temperatures was explained by an increase in the contractile properties and thus power output of muscle fibres (Beddow and Johnston, 1995; Beddow et al., 1995), whereas a high anaerobic capacity was seen in minnows (*Phoxinus phoxinus*) with enhanced burst swimming speeds and reduced vulnerability of capture by simulated trawler nets (Killen et al., 2015). Although we did not measure muscle development directly, owing to fish from the 30 and 108 dph treatments exhibiting

no increase in mass for a given length, similar results for mean speed and distance were seen for 30 and 108 dph even though 108 dph fish were smaller overall. Therefore, our results suggest that the most likely underlying mechanisms for the enhanced escape response are differences in muscle fibre properties and/or anaerobic metabolism.

Fish continuously exposed to elevated temperatures post-hatching escaped on average 34 deg clockwise compared with fish reared at present-day control temperatures. Importantly, the escape was in a direction away from the stimulus (as were the other treatments and control). The difference in direction for 108 dph fish was observed at both performance temperatures, suggesting the involvement of developmental plasticity. Exposure of 1–3 months at elevated water temperatures has previously shown effects on directionality in adult goldfish (Szabo et al., 2008) and juvenile damselfish *Pomacentrus moluccensis* (Warren et al., 2017). Non-locomotor components of the escape response are believed to be related to threat perception as well as to neurological and sensory processes (Blaxter and Fuiman, 1990; Szabo et al., 2008); consequently, it is possible that differences in the escape direction of fish from the stimulus are related to increased rates of synaptic transmission within neurological pathways (e.g. the Mauthner cells; Domenici et al., 2011; Domenici and Blake, 1997; Szabo et al., 2008).

The 2°C difference in performance temperature (28.5 or 30.5°C) did not alter escape response traits. This suggests that 28.5–30.5°C is within a temperature range that does not shift performance. The thermal sensitivity of escape performance has been found to vary between species of reef fish tested in various studies. The locomotor aspects of the escape response were not affected by short-term changes in water temperature from 29 to 31°C in three wrasse species (Motson and Donelson, 2017) or in the damselfishes *Pomacentrus moluccensis* and *P. amboinensis* (Warren et al., 2017). In contrast, the damselfish *P. wardi* exhibited reduced escape distance and speed with acute temperature change from 26.7 to 29.6°C (Allan et al., 2015). Although these differences could be species specific, they may also be due to differences in thermal range tested and where this sits within the optimal thermal performance range of each species. Further experiments with an increased range of performance temperatures would be needed to identify the threshold temperature at which escape performance is affected in *A. polyacanthus*.

Fish that developed entirely at elevated temperatures were smaller than fish from all other exposure duration treatments and the control group. Smaller body size is ecologically important in juvenile fish as it typically increases the risk of predation and reduces competitive ability (Poulos and McCormick, 2015; Goatley and Bellwood, 2016; Sogard, 1997). Reduced body size is likely due to increased energy costs for maintenance activities at higher temperatures (Munday et al., 2008; Pörtner and Knust, 2007). Although no substantial differences in body size were observed when measured at the end of the experiment in fish exposed for 3, 7 or 30 dph to elevated temperature compared with present-day control fish, we cannot conclude that there was no effect of water temperature on growth during the high temperature exposure. Either the length of exposure to high temperature had no impact on their body size, or there was an effect, after which compensatory growth occurred. Compensatory growth is common in fish following periods of stress or reduced resource availability (Ali et al., 2003), and once more-favourable conditions arise, a growth spurt occurs through recoupment of energy reserves and increased investment in structural growth (Auer et al., 2010). Our results are likely due to compensatory growth, especially for fish exposed 30 dph, as we know body size is reduced with development at elevated

temperatures (+1.5 to +3.0°C) in the first 15–30 days (Donelson et al., 2014). Compensatory growth may, however, come with negative consequences later in life, such as an increased metabolism (Crisuolo et al., 2008), reduced number of offspring (Auer et al., 2010) or a shortened lifespan (Lee et al., 2013). One aspect of the experimental set-up that may have influenced growth to be homogeneous across thermal exposure durations is that fish were raised in groups, allowing social interactions to influence body size. Interestingly, we observed a difference in body size between the sexes, with males being 1–3% smaller than females and no sex bias observed (i.e. more males). However, this sex effect was small compared with the average effect of the treatment (7–16%).

Whether critical thermal limits in fish are affected by their thermal experience is not clear from the literature. In many cases, observed differences in critical limits are attributed to methodological differences (Lutterschmidt and Hutchison, 1997; Moyano et al., 2017; Vinagre et al., 2015). For *A. polyacanthus*, the upper lethal thermal limit of 36.9 to 37.2°C that we observed did not shift as a result of post-hatching experience at elevated temperatures. This is perhaps unsurprising for this species as consistent maximum thermal limits around ~37°C have been found across populations and at different life stages (Clark et al., 2017; Rodgers et al., 2018; Zarco-Perelló et al., 2012). Moreover, where plasticity of CT_{max} has been detected, the magnitude of change is relatively small (Gunderson and Stillman, 2015; Sørensen et al., 2016; Stillman, 2003). For example, in another coral reef damselfish (*Premnas biaculeatus*), a 1.5°C increase throughout development only resulted in a 0.5°C increase in CT_{max} (Donelson, 2015). Other work has observed improvement of CT_{max} in adult coral reef damselfish (*Chromis viridis*) after 6 weeks' exposure to elevated temperatures (Habary et al., 2016). However, for Habary et al. (2016) and much of the previous published work, it is impossible to disentangle the CT_{max} obtained from the starting temperature, thus the higher values may simply be an artefact of different starting temperatures. Our work supports the growing consensus that CT_{max} are not highly plastic and suggests there is a physiological constraint around 37°C in *A. polyacanthus*.

Our study shows the response of a tropical reef fish to varying durations of marine heatwave conditions early in life. We discovered enhancements in escape performance owing to developmental plasticity when fish experienced at least the first month post-hatching at elevated temperatures. Only when elevated temperature was experienced for the full 108 days was body size reduced. We found no change in the maximum temperature that fish could survive in the short term, irrespective of the thermal exposure duration. Overall, the results suggest developmental plasticity of some traits is induced during early life if 30 days or greater warming is experienced. Marine heatwaves that last more than a month are expected to increase in frequency in the future regardless of which emissions scenario we track (Frölicher et al., 2018). The developmental changes to escape performance that result from exposure to heatwave conditions during early life may provide some benefits later in life, but may also trade off with other ecological traits, such as energy storage or reproductive development. Overall, our study improves the understanding of how marine heatwaves may impact the early development of marine fishes and their ability to persist under future global warming.

Acknowledgements

We thank MARFU technicians, especially Simon Wever and Andrew Thompson, for outstanding technical support. Thanks to volunteers Olivia Lee and Eleanor Spencer for assistance with fish husbandry and video analysis and the ARC Centre of Excellence for Coral Reef Studies for holding a writing workshop that initiated the

draft of this paper. We greatly appreciate Takahiro Shimada's advice with R and Murray Logan introducing R. K. Spinks to Bayesian analysis. Finally, thanks to the two anonymous reviewers who provided constructive feedback and improved the quality of the manuscript.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: R.K.S., P.L.M., J.M.D.; Methodology: R.K.S., P.L.M., J.M.D.; Validation: R.K.S.; Formal analysis: R.K.S.; Investigation: R.K.S.; Resources: P.L.M., J.M.D.; Data curation: R.K.S.; Writing - original draft: R.K.S.; Writing - review & editing: R.K.S., P.L.M., J.M.D.; Visualization: R.K.S.; Supervision: P.L.M., J.M.D.; Project administration: R.K.S., P.L.M., J.M.D.; Funding acquisition: P.L.M., J.M.D.

Funding

This work was supported by a King Abdullah University of Science and Technology Competitive Research Grant (CRG3 2278) and funding from the Australian Research Council Centre of Excellence for Coral Reef Studies (CE140100020). R.K.S. was supported by CRG3 2278 and P.L.M. was supported by an Australian Research Council Future Fellowship (FT130100505).

Data availability

The dataset is available on James Cook University's Tropical Data Hub repository, <http://doi.org/10.25903/5d01d448c3756>.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.202713.supplemental>

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