Marine Environmental Research 211 (2025) 107451

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

The influence of cross-generational warming on the juvenile development of a coral reef fish under ocean warming and acidification

Jasmine S. Cane [a,b,*], Yogi C. Yasutake [a,b], Shannon J. McMahon [a,c], Andrew S. Hoey [a,b], Jennifer M. Donelson [a,b]

[a] ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, 4811, Australia
[b] College of Science and Engineering, James Cook University, Townsville, QLD, 4811, Australia
[c] Marine Climate Change Unit, Okinawa Institute of Science and Technology, Onna, Okinawa, Japan

ARTICLE INFO

Keywords:
Climate change
Acanthochromis polyacanthus
Respiration
Morphology
Behaviour
Phenotypic plasticity
Adaptation

ABSTRACT

Marine ecosystems are facing escalating chronic and acute environmental stressors, yet our understanding of how multiple stressors influence individuals is limited. Here, we investigated how projected ocean warming (+1.5 °C) during grandparental (F_1) and parental (F_2) generations of the spiny chromis damselfish (*Acanthochromis polyacanthus)*, influences the sensitivity of F_3 juveniles to ocean warming (present-day vs +1.5 °C) and/or elevated CO_2 (490 μatm vs 825 μatm). After 16 weeks of exposure, aerobic physiology (resting oxygen consumption, maximum oxygen consumption, and absolute aerobic scope), behaviour (boldness and activity), and growth (length and physical condition) were measured in F_3 juveniles and the relationships between these performance traits was explored. We found that warming during F_3 development resulted in juveniles that were shorter, bolder, and in better physical condition, while elevated CO_2 resulted in shorter juveniles with a reduced resting oxygen consumption. However, across juvenile performance traits there was no interaction between ocean warming and acidification, demonstrating the additive nature of these two environmental stressors. Although we found limited signs of transgenerational plasticity, there was evidence of parental and grandparental carry-over effects which resulted in juveniles that were larger and/or in better condition when grandparents and parents experienced warming during their development regardless of the F_3 juvenile developmental treatment. These findings illustrate the significant role phenotypic plasticity has on juvenile performance under projected future climate change.

1. Introduction

Due to anthropogenic activities, marine ecosystems are increasingly exposed to a range of stressors related to climate change, with ocean warming and acidification of particular concern (IPCC, 2021). This results in environmental conditions shifting beyond those that species have historically experienced, and can cause a range of physiological, morphological, and behavioural changes, which could have significant impacts on population dynamics and ecosystem health (Brierley and Kingsford, 2009; Hoegh-Guldberg and Bruno, 2010; Doney et al., 2012). While many species may have the capacity to genetically adapt to changing environmental conditions, there are concerns that the rate of environmental change under ongoing and future climate change may outpace the capacity for genetic adaptation in many species (Chevin et al., 2010; Merilä and Hendry, 2014). This has led to the suggestion that phenotypic plasticity (the capacity of a genotype to render alternate phenotypes; Pigliucci, 2001) may allow individuals to maintain performance under altered environmental conditions (Hoffmann and Sgró, 2011; Munday et al., 2013).

Phenotypic plasticity can be induced by environmental conditions experienced by both the current and past generations. Within a generation, developmental plasticity can occur in response to environmental conditions experienced during early ontogeny and is generally considered to be permanent (West-Eberhard, 2003; Angilletta, 2009). While early life stages of fish are generally more sensitive to abiotic changes (Pankhurst and Munday, 2011), experiences during this time also have greater potential to produce plasticity due to epigenetic sensitivity (Burton and Metcalfe, 2014; Jonsson and Jonsson, 2014; O'Dea et al., 2016). Additionally, climate change will occur over multiple generations, potentially allowing for transgenerational plasticity and

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* Corresponding author. ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, 4811, Australia.
E-mail address: jasmine.cane@my.jcu.edu.au (J.S. Cane).

https://doi.org/10.1016/j.marenvres.2025.107451
Received 12 March 2025; Received in revised form 26 July 2025; Accepted 13 August 2025

carry-over effects (Rummer and Munday, 2017; Donelson et al., 2018). While both transgenerational plasticity and carry-over effects are used to describe differences in offspring's phenotype in response to conditions experienced by previous generations, transgenerational plasticity is reserved for when offspring phenotype interacts with the current environment (Salinas et al., 2013; Donelson et al., 2018), while carry-over effects occur regardless of offspring environment (Jablonka et al., 1995; Bonduriansky and Crean, 2018; Donelson et al., 2018). Whether plasticity is produced in relation to environmental change can depend on the costs of sensing and responding to change relative to the direct costs of being exposed to the stressor (Angilletta, 2009). Disentangling the effects of developmental and transgenerational plasticity, while difficult, can be achieved if the current generation did not experience the historical environmental conditions during primordial germ cell development or embryogenesis (Donelson et al., 2018).

Ocean warming is considered one of the greatest threats to marine ecosystems due to the majority of species being ectothermic and lacking internal temperature regulation (Huey and Stevenson, 1979; Huey and Kingsolver, 1989). Temperature increases as small as 1–3 °C above the present-day summer average have been found to reduce the aerobic scope (Nilsson et al., 2009; Johansen and Jones, 2011; Slesinger et al., 2019), growth (Munday et al., 2008; Motson and Donelson, 2017; Watson et al., 2018), and reproduction of marine fish (reviewed in Pankhurst and Munday, 2011), as well as alter their anti-predator behaviour (Lienart et al., 2014; Motson and Donelson, 2017). Marine organisms are also vulnerable to ocean acidification as the ocean absorbs about 20 % of anthropogenic CO_2 emissions per year (IPCC, 2021). This dissolved CO_2 decreases ocean pH, and the availability of dissolved carbonate and bicarbonate ions (Schunter et al., 2022). Compared to ocean warming, the effects of ocean acidification on marine fishes are generally less and more variable, both within and among species (Lefevre, 2016, 2019). While this variation has been found across range of performance traits including metabolic rate (Couturier et al., 2013; Rummer et al., 2013; McMahon et al., 2020) and growth (Baumann et al., 2012; Miller et al., 2012; McMahon et al., 2019), the effects of elevated CO_2 on fish behaviour have been more consistent. Relatively high levels of dissolved CO_2 (750–1100 μatm) alter the responses of fishes to auditory (Simpson et al., 2011; Rossi et al., 2016), olfactory (Munday et al., 2009), and physiochemical cues (Welch et al., 2014; Pistevos et al., 2017; McMahon et al., 2018). Previous studies have found that these negative effects of climate change, such as ocean warming, can be mitigated (or reduced) when the current generation is exposed to conditions from early life, or when previous generations are exposed to these conditions (Donelson et al., 2012b; Grenchik et al., 2013; Shama et al., 2014). However, the nature of the plasticity can depend on the timing and magnitude of thermal exposure (Donelson et al., 2016; Bernal et al., 2022; Spinks et al., 2022).

Knowledge to date on the capacity for plasticity in marine fishes in response to climate change is primarily based on single environmental stressors, however, this approach oversimplifies the complexities organisms will face as climate change advances. The extent and timing of environmental change are not expected to be uniform across the world's oceans (IPCC, 2014; IPCC, 2021). As a result, marine species may be exposed to multiple environmental stressors simultaneously or sequentially within a lifetime, or among generations, making the response in future environmental conditions difficult to predict based on single-stressor studies (Ghedini et al., 2013; Gissi et al., 2021). For instance, exposure to one stressor may prime an organisms' system to handle another stressor (Gunderson et al., 2016). Alternatively, organism's may be more susceptible to a stressor when it is superimposed on an existing one (Nyström et al., 2001). When ocean warming and acidification have been investigated simultaneously during early life, the effects on aerobic physiology and growth of marine fishes have generally been found to be either additive (Munday et al., 2009; Miller et al., 2012; Flynn et al., 2015) or synergistic (Miller et al., 2012; Laubenstein et al., 2019). Considering the complexity of multi-stressor impacts and the critical role of plasticity in coping with climate change, testing more ecologically realistic scenarios is essential.

This study builds on previous multigenerational work investigating thermal plasticity in the coral reef damselfish *Acanthochromis polyacanthus*, by investigating whether thermal experience of previous generations influences the sensitivity to multiple environmental stressors in the current generation. The spiny chromis (*A. polyacanthus)* is a widespread Indo-Pacific species with populations ranging from the southern Coral Sea to the southern Philippines (15°N–26°S and 116°E–169°E; Allen, 1991). *A. polyacanthus* form monogamous breeding pairs that last throughout the Austral summer breeding season (most often between October and February; Robertson, 1973). Both parents care for and defend the eggs which are laid on the substrate (Kavanagh, 2000). *A. polyacanthus* lack a dispersive pelagic larval phase and instead, juveniles remain with their parents up to 45 days after hatching (Kavanagh, 2000). Previous research on *A. polyacanthus* has found that exposure to elevated temperature during development and post-maturation had negative effects on reproductive output and offspring quality during the first breeding season (Spinks et al., 2021). However, with further exposure to elevated temperature (i.e. second breeding season; additional 1 year) improved the reproductive output; demonstrating that the adverse effects of warm temperature can be mitigated with extended exposure (Yasutake et al., 2025). Building on this work, we expect that warming in the F_1 grandparent and F_2 parent generations may improve thermal performance of F_3 juvenile *A. polyacanthus* when they also develop in warm conditions (Spinks et al., 2021; Yasutake et al., 2025). Prior thermal exposure may also impact F_3 juveniles' sensitivity to elevated CO_2, or it may alter the trade-offs between performance traits (as seen in Laubenstein et al., 2019). The findings of this investigation will therefore further our understanding of how juvenile reef fish respond to multiple climate changes across generations.

2. Materials and methods

2.1. Cross-generational experimental design

Wild adult *A. polyacanthus* used in this experiment were collected from the Palm Island region (18°40–45′S, 146°34–41′E) in 2014, and from Bramble Reef (18°24′S, 146°42′E) in 2015 and transported to the Marine and Aquaculture Research Facility at James Cook University, Townsville, Australia (F_0 generation; see Spinks et al., 2021 for more details). Two temperature treatments were used in this three-generation experiment: 1) Control treatment in which water conditions simulated seasonal temperature cycles (winter: 23.2 °C, summer: 28.5 °C) for the Palm Islands region of the Great Barrier Reef (AIMS, 2016), and 2) Warm treatment in which water conditions simulated +1.5 °C than present-day (winter: 24.7 °C, summer: 30 °C, as per Spinks et al., 2021) to represent predicted temperatures for 2050–2100 under climate change (Collins et al., 2013; IPCC, 2021). Both temperature treatments included a diurnal temperature cycle (0300 h −0.6 °C, 1500 h + 0.6 °C) matching the natural daily temperature cycle of the Palm Island region (shallow reef; Spinks et al., 2021). All fish were housed in environmentally controlled laboratories for the duration of the experiment (see S.M 2.1. for further detail about the adult fish system and husbandry).

F_0 *A. polyacanthus* adults were housed in breeding pairs within 60 L aquaria with a half terracotta pot for shelter and egg deposition. Pairs were maintained at seasonally fluctuating present-day Control conditions. In the Austral summer of 2015–2016 the first clutch (F_1) from the six wild-caught pairs were produced at Control conditions (~28.5 °C) and split at hatching into the two temperature treatments Control and Warm +1.5 °C (Fig. 1). These F_1 fish were maintained in sibling groups at these two temperature treatments throughout development until 1.5 years of age, at which time each sibling group was divided further into Control, or Warm temperature conditions creating four treatments throughout post-maturation (Fig. 1; Spinks et al., 2021). As the F_1 fish

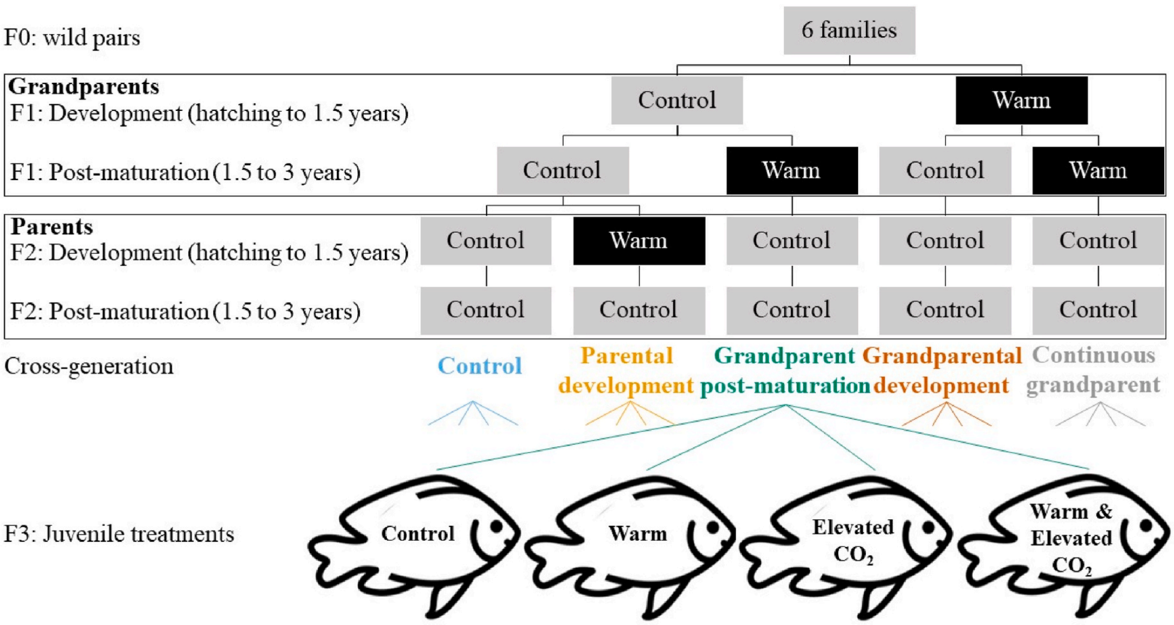

Fig. 1. Cross-generation experimental design outlining the thermal experience of F_1 grandparent and F_2 parent generations. F_3 offspring from the five cross-generational groups were crossed between 4 development treatments including Control (28.5 °C, 490 µatm); Warm temperature (30 °C, 490 µatm); Elevated CO_2 (28.5 °C, 825 µatm); and Warm temperature and Elevated CO_2 (30 °C, 825 µatm).

approached 3 years of age non-sibling pairs were formed from male and female fish maintained at the same treatment conditions during both development (i.e., hatching to 1.5 years) and post-maturation (1.5–3 years), in September 2018. In each of the four treatments, three to five F_1 adult pairs contributed a clutch to the F_2 generation. The first clutch of offspring (F_2) produced by F_1 breeding pairs in the Austral summer of 2018–2019, were split at hatching into both Control and Warm temperature conditions and reared to 1.5 years as described above for the F_1 generation, creating eight treatments (Fig. 1; Yasutake et al., 2025). These F_2 fish were maintained at their respective treatment conditions until 1.5 years of age (post-maturation) when all F_2 adults were transferred to Control temperature conditions and maintained until 3 years of age for the current experiment.

Adult F_2 fish were allocated into non-sibling pairs with fish from the same treatment beginning in late August 2020 (at ~2 years of age) and where possible, further pairs were made in December 2021 for the current experiment. Of the possible eight cross-generational thermal experience combinations, five were used to produce F_3 offspring in this experiment (Fig. 1): Control (n = 5 pairs); Parental development in Warm temperature (n = 5 pairs); Grandparent post-maturation in Warm temperature (n = 5 pairs); Grandparental development in Warm temperature (n = 5 pairs); Continuous grandparent in Warm temperature, (n = 3 pairs; n's indicate the number of unique pairs that produced F_3 offspring utilized in this study).

2.2. *F_3 juvenile experimental design*

When summer average water temperature (Control: 28.5 °C) was reached in November 2021, terracotta pots were checked daily for newly laid egg clutches. Once an egg clutch was recorded, it was checked daily for the presence of hatched offspring (F_3), which generally occurs in the afternoon for this species around 9 days after eggs are laid (Donelson et al., 2010). Newly hatched offspring from all clutches were randomly divided into groups of 20 individuals and placed in aerated 2 L holding containers within 32 L tanks which were maintained at one of four juvenile treatments. To facilitate a slow transition to the treatment conditions, water from the tank was gradually added into the holding containers over 4–12 h, after which juveniles were released into the tank. If there was any mortality during this transition time, those individuals were replaced to achieve a starting tank density of 20 individuals.

Juvenile F_3 treatments included the Control (28.5 °C, 490 µatm), Warm temperature, (30 °C, 490 µatm), Elevated CO_2 (28.5 °C, 825 µatm), and Warm temperature and Elevated CO_2 (30 °C, 825 µatm; Table S1). These values were selected to reflect the most likely future scenarios (SSP1-2.6 and SSP2-4.5) under the CMIP6 model end-of-century projections (Kwiatkowski et al., 2020; IPCC, 2021). For all five cross-generational thermal experience combinations, clutches of up to n = 5 pairs were used for this experiment. In the case of the Continuous grandparent cross-generation only three pairs reproduced, and two clutches were used from one pair. For each clutch n = 2 replicate tanks were made per each of the four juvenile treatments. Juvenile environmental conditions were controlled and supplied by four recirculating seawater systems (see S.M 2.2. for aquaria detail and Table S1 for water quality parameters). *A. polyacanthus* were fed a high food ration; ~2–4 % of body weight, once per day. From hatching, juveniles were fed live Artemia nauplii and were slowly weaned onto INVE Aquaculture Nutrition NRD pellets. Pellet size increased over time as fish grew and developed over the duration of the experiment (S.M 2.2.). Fish were grown in sibling groups under the four juvenile treatment conditions until ~120 days old.

2.3. *Aerobic physiology*

Between 101 and 137 days post-hatching (dph), the aerobic physiology of four juveniles from each tank (n = 8 juveniles per clutch per F_3 treatment; n = 580; Table S2) was measured using intermittent flow respirometry under their juvenile treatment's conditions (S.M 2.3.). Prior to respirometry, fish were starved for 12–24 h to ensure that measurements were not affected by additional metabolic functions such as digestion (Niimi and Beamish, 1974). Resting (MO_{2rest}) and maximum (MO_{2max}) oxygen consumption was tested and used as a proxy for metabolic performance and the energy available for both internal biological process and higher-level functions like swimming, growth and reproduction (Pörtner, 2001; Clarke and Fraser, 2004; Lefevre, 2016). Fish were placed in a circular swim chamber (S.M 2.3.) for 3 min of aerobic swimming, which was then followed by 1 min of air exposure (Clark et al., 2013). Fish were then placed in a randomly allocated glass or clear plastic respirometry chamber purposely built for juvenile fish of this size (between 32 and 70 ml). Respirometry chambers, run in groups of four, were submerged in 52 L aquaria which received constant flow from the system with the respective juvenile treatment conditions and aeration (see S.M 2.3. for chamber and aquaria specifications). Juveniles remained in the chambers while a purpose-built python program (AquaResp v3.0) was used to control the timing measurement cycle. This consisted of a 1 min wait period, a 3 min measurement period, and a 3 min flushing period to return oxygen levels to ~100 % (measured by a PyroScience Optical Oxygen Meter; S.M 2.3.). This 5 min cycle was repeated continuously during the 3 h trial duration allowing the fish to come to rest for resting oxygen rate; MO_{2rest} (Clark et al., 2013; Killen et al., 2014; Laubenstein et al., 2019).

Maximum oxygen consumption, MO_{2max}, was calculated manually from the steepest rate of oxygen decline in 60 s blocks, from the periods 1–60, 31–90, 61–120, 91–150, and 121–180 s in either of the first two 3 min measurement cycles. This was put into the equation:

$$MO_2 = K * V * \beta / M$$

(McMahon et al., 2020; S.M 2.3.). Resting oxygen consumption was calculated using the MO_2 values generated from the python program (AquaResp V3.0) during the 3 h trial. After average background respiration was subtracted, MO_2 values below 0.9 R^2, and outside 2 standard deviations (SD) of the average were removed and only the lowest 10 values (of the 3 h trial) were then averaged to generate MO_{2rest} for each fish (Clark et al., 2013; Laubenstein et al., 2020). After all data was collated, individuals ±2 SD of the mean MO_{2rest} and MO_{2max} were excluded from the data set. Absolute aerobic scope (MO_{2max} - MO_{2rest}) was also calculated for each fish.

2.4. Behavioural tests

Behaviour traits were measured for the same individuals that underwent respirometry trials (n = 544; Table S2) to indicate juvenile survival through foraging success and predation evasion (Metcalfe et al., 2016). Directly after the completion of their respirometry trial, juveniles were placed in 75 L holding tanks that were set at their respective treatment conditions. To keep track of individual fish, they were maintained within fine mesh 3 L breeding baskets within each of the holding tanks. If juveniles finished respiratory trials before 2 p.m. (and required >18 h holding before behaviour trials) juveniles were fed newly-hatched *Artemia* nauplii at a concentration of 1 individual 5 ml^{-1} to prevent starvation. For a single clutch, respirometry treatment timing (am or pm) alternated over the 2 days to balance any effect of feeding prior to the behaviour trials. The day following respiration trials, fish were placed into one of three identical square white behaviour arenas (300 × 300 × 150 mm) filled with 7 L of water from of their respective treatment conditions (water height 75 mm), which contained newly-hatched *Artemia* nauplii at a concentration of 1 individual 5 ml^{-1} to encourage movement. Larval and juvenile fish are known to quickly recover from activity, and as such, behavioural tests have commonly been conducted the day following respirometry trials (Killen et al., 2014). To commence the trial, fish were placed into a shelter (5-way 25 mm PVC joint) in the centre of the arena that was surrounded by circular tube (100 mm diameter PVC) and allowed to habituate for 10 min. At the start of the behaviour trial, the habituation cover was slowly and carefully removed, and movement of the fish was recorded for 15 min using a digital video camera that was mounted above the tank for an aerial view (GoPro Hero: 3 or Session). Throughout the trial period the behaviour experimental conductor (always YCY) was absent from the room. Videos were analysed by the primary investigator (JSC) blinded to the cross-generational and juvenile treatments. From the videos, the combination of boldness and activity behaviour were scored on a scale from 1 to 5, with 1 being the least and 5 being the most bold and active (hereafter known as behaviour score; Table 1).

2.5. Morphological metrics

Morphometric traits of standard length and wet weight were measured for all F_3 juveniles (n = 2955; Table S2) as body size (growth) is a key trait related to competitive ability against conspecifics and predators (Booth and Beretta, 2004; Hoey and McCormick, 2004; Poulos and McCormick, 2015). Following the physiological and behavioural testing outlined above, all tested juveniles were euthanised with an overdose of clove oil and sea water (1:20) and then preserved in 75 % ethanol. All remaining juveniles that did not undergo respirometry and behavioural testing were euthanised and preserved as above at a slightly later age (+1–13 days). Standard length was measured with digital callipers to the nearest 0.01 mm, and weight to the nearest 0.0001 g (Shimandzu ATX224), for each fish post-preservation. In this study, the relative weight for a given standard length was used as a proxy for physical condition, as opposed to the criticised Fulton's K condition index (Jones et al., 1999; Froese, 2006; Nash et al., 2006).

2.6. Statistical analysis

The effect of cross-generational thermal experience, juvenile developmental temperature, and juvenile developmental CO_2 conditions, on the morphology of the F_3 generation was modelled in R (version 4.2.2) with linear mixed effects model (using lmer within the LME4 package; Bates et al., 2015). For all analyses in this study, during model selection the inclusion of additional model covariates (density, tank number, parental clutch ID, or time of day: am/pm) were sequentially explored and the model's goodness of fit was compared using analysis of variance (ANOVA; Pathak et al., 2013). Covariates were included if they improved the model fit (as per Fisher et al., 2015; LaMonica et al., 2021). Model selection did not undertake a step-wise backward selection process of the main factors of interest (cross-generation thermal experience, juvenile development temperature, and CO_2). Firstly, significant kurtosis (5.25) was evident in the standard length data set, therefore data points outside the interquartile range were removed. Both this reduced data set, and the full data set produced the same overall model results and significance. Standard length was then modelled as the dependent variable with cross-generation, temperature, and CO_2 treatments entered the model as fixed factors. Tank number, maternal lineage (maternal grandfather and grandmother code A-F), and paternal lineage (paternal grandfather and grandmother code A-F) were also included into the models as random factors.

The physical condition model had log weight (g) being the dependent variable with cross-generation, temperature, CO_2 treatments, and log length (mm) included in the model as fixed factors. Tank number, tank density, maternal lineage, and paternal lineage were also included

Table 1
Combined boldness and activity (behaviour) score given to each individual juvenile during the 15min behaviour trial with description of the behaviour.

Score	Description	Details
1	Stationary in tunnel/ shelter or in corner	Little to no movement, stays in same spot for the entirety of the video recording
2	Stationary in multiple places along walls	No more than five moves to another spot on the wall, sticks very close to the wall
3	Swimming along walls	Always close to the walls; may swim up and down to change spots (includes swimming along the wall at up to one body length distance)
4	Ventures to the middle	Comes far off the wall for exploration (greater than one body length). Or swimming to the other side of the tank, crossing close to or above the tunnel
5	Often swimming around in the middle	Swimming around for the majority of the video recording

into the models as random factors. Five influential data points that were disproportionally impacting the model fit were examined using Cook's distance (Bochdansky et al., 2005; Bernal et al., 2022) and were removed from the final statistical analysis. Models were also run with all data included and did not change output significance.

During rearing there was natural mortality across treatment groups which is known to influence food availability and size structure (Holm et al., 1990; Brockmark and Johnsson, 2010). Juvenile survival was analysed using an independent generalised linear mixed effect model, glmer (Bates et al., 2015) with a binomial distribution and logit-link function (logistic regression). The number of fish present at the end of the experiment versus the number missing was the dependent variable, while cross-generational thermal experience, temperature treatment, and CO_2 treatment were fixed factors. Maternal lineage, and paternal lineage were also included into the models as random factors.

The physiology of juveniles was analysed with linear mixed effects model (as above). Prior to model analysis, four fish that were disproportionality heavier (>75 % mean weight) than the rest of the data (observed from raw data qqplots) were removed from the data set. Resting oxygen consumption, maximum oxygen consumption, and aerobic scope were separately modelled as the dependant variable with cross-generation thermal experience, temperature, and CO_2 treatments as fixed factors. Respirometry chamber ID, maternal lineage , and paternal lineage were also included into the models as random factors. It was concluded that covariates did not improve model fit and were therefore not included in the final models (Fisher et al., 2015; LaMonica et al., 2021). Aerobic scope underwent a square root transformation to better adhere to the model assumptions of a gaussian distribution.

Prior to model analysis of the behaviour data, the number of individuals under each behaviour score (1–5) was counted for each clutch. This count data was then analysed using a negative binomial regression model (glm.nb within the MASS package; Venables and Ripley, 2002). The count value was used as the dependent variable with cross-generation, temperature, CO_2 treatment, and the behaviour score category (1–5) as fixed factors. Model assumptions of linearity, residual fit, and lack of over-dispersion and zero-inflation were met. Raw data was plotted using ggplot2 to generate the proportional count of individuals per behaviour score.

The interrelationship between behaviour score and physiology (MO_{2rest} and aerobic scope) was also analysed with a linear mixed effects model. MO_{2rest} or aerobic scope were the dependent variable, and cross-generation thermal experience, temperature, CO_2 treatments and behaviour score were entered into the model as fixed factors. Parental number (clutch ID; allowing identification of siblings) and Respirometry chamber ID were included into both models as a random factor.

For all linear mixed effects models, assumptions including linearity, normality, and homogeneity of residuals, were visually assessed with Q-Q plots and frequency distributions. Following construction of models, main effects were determined with a Wald chi-square test (II, car package). If there was a significant interaction between two or more factors, relevant pairwise comparisons were made with estimated marginal means and Tukey method of p-value adjustment ($p < 0.05$; lmer, glm. nb, and glmer models, emmeans package). Estimated marginal means and standard errors are depicted in the figures for physiological and morphological traits. The fitted data values are depicted in figures for the interrelationship between behaviour score and physiology.

3. Results

3.1. Morphology

Linear growth (standard length) of juvenile *A. polyacanthus* was affected by juvenile temperature ($X^2 = 7.99$, df = 1, P = 0.005), CO_2 ($X^2 = 7.83$, df = 1, P = 0.005), and cross-generational thermal experience ($X^2 = 35.55$, df = 4, P < 0.001), but not their interactions (Fig. 2A, Table S3B). Juveniles that developed in Warm temperature were on average 1.86 % shorter than those in the Control temperature. Juveniles reared in Elevated CO_2 were also shorter than those reared in Control conditions by 1.56 %. Irrespective of juvenile treatment conditions, juveniles from the Control cross-generation were 6.73 % and 6.15 % shorter compared to the Grandparental development and Continuous grandparent cross-generation, respectively (P < 0.001).

Juvenile physical condition (weight for a given standard length) was also influenced by juvenile temperature ($X^2 = 26.71$, df = 1, P < 0.001)

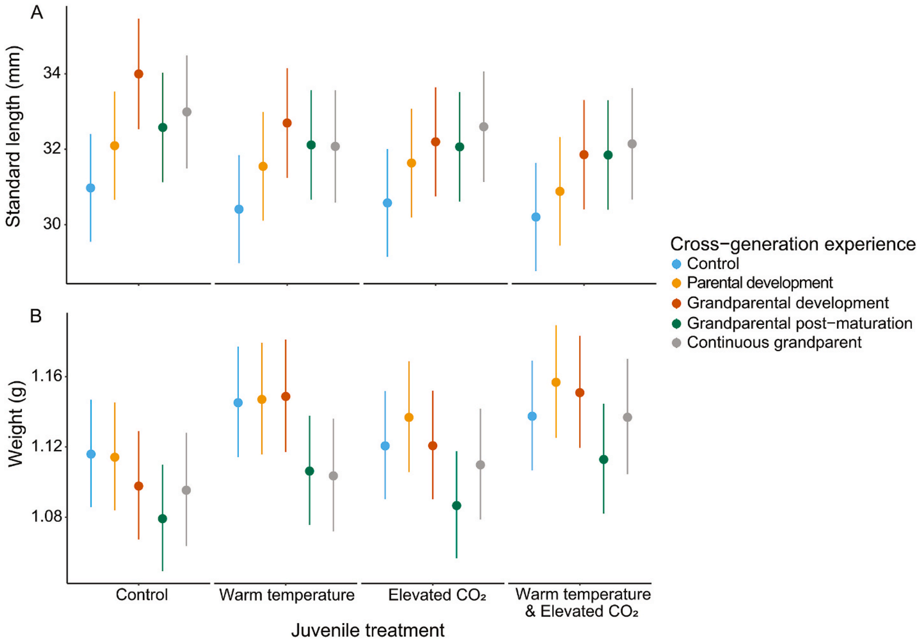

Fig. 2. Standard length (A) and physical condition in terms of weight for a given standard length (B) of juvenile *A. polyacanthus* maintained at Control (28.5 °C, 490 µatm); Warm temperature (30 °C, 490 µatm); Elevated CO_2 (28.5 °C, 825 µatm); or Warm temperature and Elevated CO2 (30 °C, 825 µatm) for 101–137 days post-hatching. All data is the estimated marginal means ± SE. In the case of physical condition this estimated marginal mean of weight is for the average standard length of 31.2 mm.

and cross-generational thermal experience ($X^2 = 12.48$, df = 4, P = 0.014), but not CO_2 ($X^2 = 3.55$, df = 1, P = 0.06). There were also no interactions among factors (Fig. 2B, Table S4B). In contrast to standard length, juveniles that developed in Warm temperature were on average in better condition (2.4 % heavier for a given length) than those in present-day Control temperature. The effect of cross-generation thermal experience on juveniles was seen in those from Grandparental post-maturation cross-generation being in poorer condition than those fish from the Grandparental development (P = 0.04) and Parental development cross-generation but this was not significant (P = 0.051).

Survival of fish was influenced by juvenile temperature, CO_2, and cross-generational experience (Cross-generation × Temperature × CO_2: $X^2 = 11.45$, df = 4, P = 0.022; Fig. 3, Table S5). Within the Control juvenile treatment, the probability of survival for juveniles from the Grandparental development cross-generation was 13–18 % lower than juveniles from all other cross-generation treatments (Control and Parental development $P < 0.01$). Juveniles from Grandparental development cross-generation also differed in survival across juvenile developmental treatments with the probability of survival reduced in Control and Warm conditions compared to juveniles in the Elevated CO_2 (all $P \leq 0.002$).

3.2. Physiology

The resting oxygen consumption (MO_{2rest}) of juvenile *A. polyacanthus* was significantly affected by juvenile CO_2 conditions ($X^2 = 4.97$, df = 1, P = 0.026; Fig. 4A, Fig. S1), but not juvenile temperature ($X^2 = 0.31$, df = 1, P = 0.576), cross-generational thermal experience ($X^2 = 2.00$, df = 4, P = 0.735), or their interaction (Table S6B). The MO_{2rest} was on average 2.6 % lower for juveniles that developed in elevated CO_2 conditions than those reared in present day CO_2 conditions.

Maximum oxygen consumption was influenced by the cross-generation thermal experience and CO_2 (Cross-generation × Temperature × CO_2: $X^2 = 13.80$, df = 4, P = 0.008; Table S7B). Overall, the general pattern was that the Parental development, Grandparent post-maturation, and the Grandparental development cross-generation all had similar MO_{2max} across the four juvenile treatments, while juveniles from the Continuous grandparent cross-generation and the Control cross-generation showed variation depending on the F_3 juvenile environment (Fig. 4B). However, within the Warm temperature and Control CO_2 juvenile treatment, the Continuous grandparent cross-generation appeared to have a greater MO_{2max}, but it was not significantly different from those within the same development treatment (Cross-generation × Temperature × CO_2: all post-hocs $P > 0.05$).

Juvenile aerobic scope exhibited similar patterns to MO_{2max}, with differences due to cross-generation thermal experience, particularly in juveniles from the Continuous grandparent cross-generation within the Warm temperature and Control CO_2 juvenile treatment (Cross-generation × Temperature × CO_2: $X^2 = 10.66$, df = 4, P = 0.031; Fig. S2, Table S8B).

3.3. Behaviour

The behaviour score of juvenile *A. polyacanthus* was affected by developmental temperature ($X^2 = 5.58$, df = 1, P = 0.02). In the Control treatment, juveniles predominantly had a behaviour score of 3 whereas in the Warm treatment, juveniles predominantly had a score of 4 indicating greater boldness and activity (Fig. S3). Neither juvenile CO_2 treatment, cross-generation, nor interactions among treatments affected the behaviour score of juvenile *A. polyacanthus* (Fig. 5; Table S9).

3.4. Physiology and behaviour interrelationship

The relationship between MO_{2rest} and behaviour score depended on juvenile CO_2 conditions ($X^2 = 4.83$, df = 1, P = 0.028) but not temperature ($X^2 = 0.20$, df = 1, P = 0657; Table S10B). Under Control CO_2 conditions, shy (low score) fish had a higher MO_{2rest} than bold (high score) fish, whereas under Elevated CO_2 conditions shy fish had a lower MO_{2rest} than bold fish, while bold and active fish, regardless of development CO_2 conditions, had similar MO_{2rest} (Fig. S4). However, there was also an interaction between behaviour score, cross-generational experience, and juvenile CO_2 treatment ($X^2 = 11.40$, df = 4, P = 0.022). Specifically, juveniles from the Control cross-generation exhibited the strongest interaction between MO_{2rest} and behaviour score depending on CO_2 conditions, and thus the overall pattern of CO_2 significance is driven largely by this cross-generational experience (Fig. 6).

The relationship between aerobic scope and behaviour score was influenced by juvenile developmental temperature ($X^2 = 4.28$, df = 1, P = 0.039; Fig. 7). Under Warm temperature, shy fish had a higher aerobic scope than bold fish. Whereas under Control temperature, aerobic scope did not differ between shy and bold fish. Bold and active fish (with a high behaviour score) had similar aerobic scope regardless of developmental temperature (Table S11B).

4. Discussion

Juvenile *Acanthochromis polyacanthus* phenotypes were influenced by developmental conditions, both water temperature and CO_2, and historical cross-generation experience of thermal conditions by parents and grandparents. Juvenile *A. polyacanthus* that developed under elevated temperature were shorter, bolder, and in better physical condition, whereas juveniles that developed in elevated CO_2 were shorter but had a lower resting oxygen consumption rate, compared to juveniles from the control treatment. Exposure to warm temperatures in the parental or grandparental generations during their development produced juveniles that were larger and in better condition (carry-over effects) and this was not affected by exposure to the novel environmental

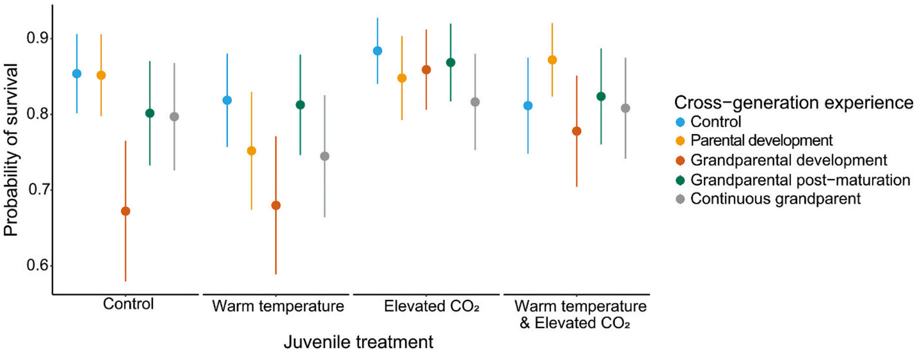

Fig. 3. Probability of for juvenile *A. polyacanthus* surviving 101–137 days post-hatching at Control (28.5 °C, 490 μatm); Warm temperature (30 °C, 490 μatm); Elevated CO_2 (28.5 °C, 825 μatm); or Warm temperature and Elevated CO_2 (30 °C, 825 μatm). All data is the probability ± SE.

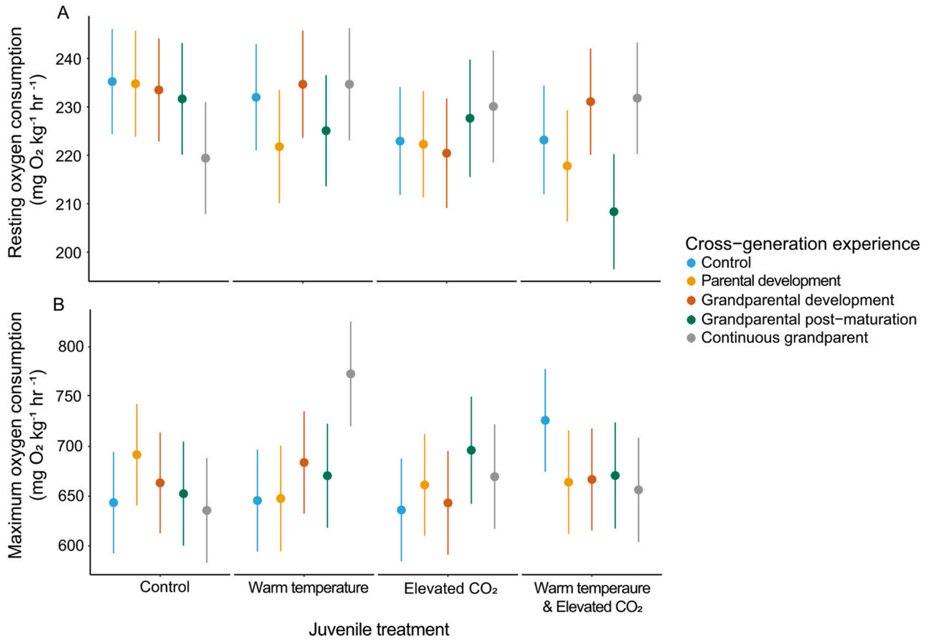

Fig. 4. Resting oxygen consumption (A) and maximum oxygen consumption (B) of juvenile *A. polyacanthus* maintained at Control (28.5 °C, 490 μatm); Warm temperature (30 °C, 490 μatm); Elevated CO_2 (28.5 °C, 825 μatm); or Warm temperature and Elevated CO_2 (30 °C, 825 μatm) for 101–137 days post-hatching. All data is estimated marginal means in mg O_2 kg^{-1} hr^{-1} ± SE.

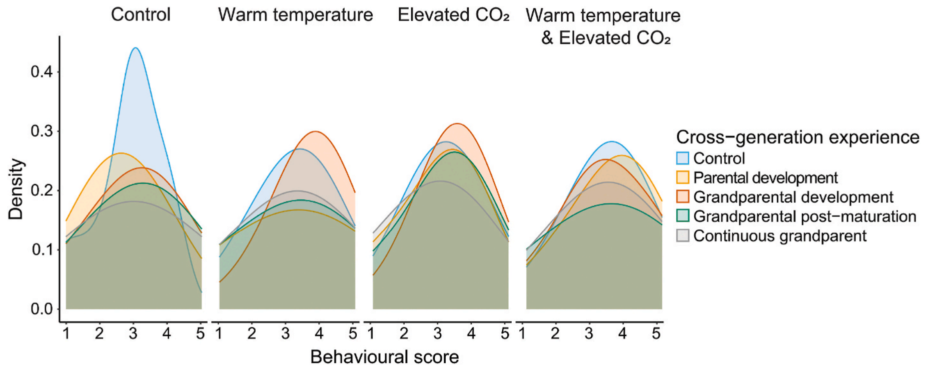

Fig. 5. Proportional density juvenile *A. polyacanthus* at each combination behaviour (boldness and activity) score. Juveniles were maintained at Control (28.5 °C, 490 μatm); Warm temperature (30 °C, 490 μatm); Elevated CO_2 (28.5 °C, 825 μatm); or Warm temperature and Elevated CO_2 (30 °C, 825 μatm) for 101–137 days post-hatching.

stressor of elevated CO_2. There was also some evidence for transgenerational plasticity with enhanced maximum oxygen consumption (and subsequently aerobic scope) by juveniles from the grandparents exposed continuously to warming, only when the juveniles developed in warm temperature. On the other hand, we also found reduced survival in juveniles from grandparents exposed to warming during development when juveniles were exposed to present-day CO_2. These complex patterns of carry-over and transgenerational plasticity highlight the variety of plastic phenotypic outcomes that may arise under future environmental conditions.

CO_2 fluctuations are naturally experienced over short-time scales on coral reefs (Hannan et al., 2020). Specifically, pCO_2 was found to range from 283.6 to 554.5 μatm across 9 days on three reefs at Lizard Island on the Great Barrier Reef. Consequently, the reduced resting metabolic rate under elevated CO_2 conditions observed here and previous studies (Rummer et al., 2013; Hannan et al., 2020) might indicate plasticity in response to moderate increases in CO_2. A reduction in resting metabolic rate would be expected to provide energetic savings that can be directed to other activities such as growth, and while there was some increase in weight for a given standard length (~1 % increase in physical condition), there was a greater and significant reduction in standard length (~1.56 %) when juveniles developed in elevated CO_2. Reductions in juvenile growth following developmental exposure to elevated CO_2 is analogous with previous studies (Baumann et al., 2012; Miller et al., 2012; McMahon et al., 2019) and concurrent shifts in metabolic traits have not always been observed (Miller et al., 2012). Energetic costs and trade-offs during development may have occurred in the elevated CO_2 treatment, whereby producing plasticity to achieve reduced resting metabolic rate and improved physical condition, came at a cost to standard length.

Development in warm water resulted in shorter and bolder fish that were in better physical condition, regardless of developmental CO_2 and previous cross-generational thermal experience. These thermally induced phenotypic changes have the potential to provide enhanced survival in nature, since bolder and more active individuals can have increased foraging success (Metcalfe et al., 2016) and individuals with enhanced physical condition may be selected for in nature through reduced predation (Booth and Beretta, 2004; Hoey and McCormick, 2004; Poulos and McCormick, 2015). Theory suggests that behavioural, physiological, and life-history traits can covary, and due to trade-offs,

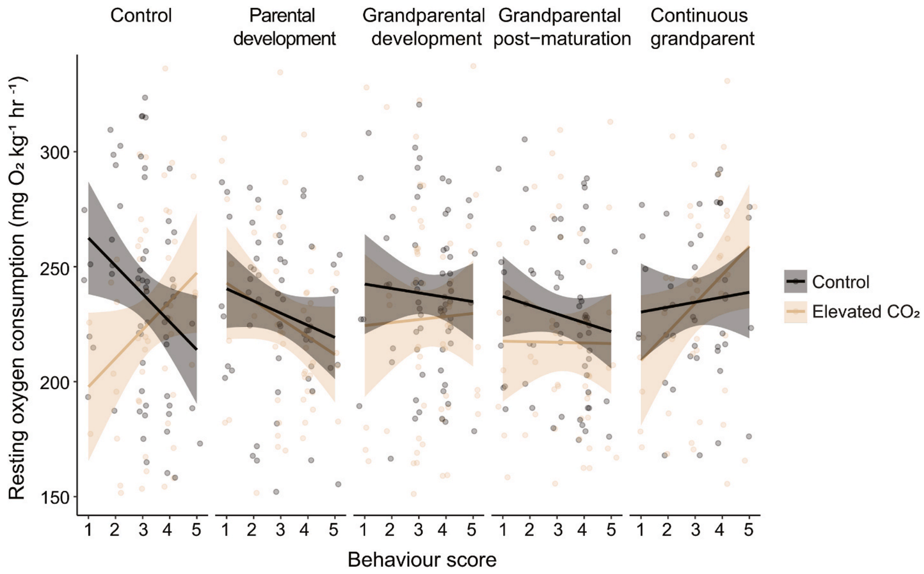

Fig. 6. Resting oxygen consumption of juvenile *A. polyacanthus* maintained at Control (490 µatm, 28.5 °C, or 30 °C); Elevated CO_2 (825 µatm, 28.5 °C, or 30 °C) at each behaviour (boldness and activity) score. Fitted data points are displayed with a linear trendline (with a smoothing function in ggplot2) for each cross-generation.

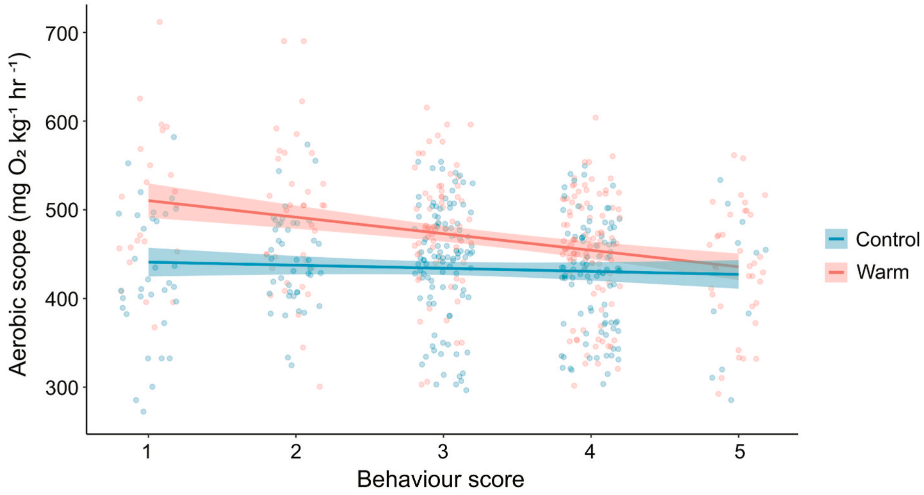

Fig. 7. Aerobic scope of juvenile *A. polyacanthus* maintained at Control (28.5 °C); Warm temperature (30 °C) for 101–137 days post-hatching at each behaviour (boldness and activity) score. Fitted data points are displayed with a linear trendline (Control: $y = 440–3.5x$, $R^2 = 0.003$; Warm: $y = 530 + 19x$, $R^2 = 0.086$).

combinations of traits will exist along a fast-slow continuum (Pace--of-life theory; Binder et al., 2016; Réale et al., 2010; Tüzün and Stoks, 2022). Furthermore, varying trait combinations can occur between populations depending on environmental conditions with risk-prone, fast-paced life strategy enabling individuals to outcompete conspecifics, allowing greater access to resources such as food, habitat, and mates (Goulet et al., 2017; Hämäläinen et al., 2021). Traits of fish developing in warm temperature, including increased behaviour score and greater weight for a given standard length, is likely to benefit them in a future ocean with increased costs (e.g. swimming, reproduction, competition, and energy storage; Doney et al., 2012) and reduced food availability (Richardson, 2008; Goulet et al., 2017; Hämäläinen et al., 2021). This covariance of life history traits with thermal exposure is expected to be stronger for early-life stages and in predictable stable environments like the tropical oceans (Polverino et al., 2018; Hämäläinen et al., 2021). However, this theory has only been explored in a limited number of studies and support has been mixed due to inconsistencies in experimental design, behaviour categorisation, consideration for life history traits, and effects of metabolism (reviewed in Gopal et al., 2023). Here, while our experimental design considered many of these challenges, we still found no clear relationship to support the pace-of-life syndrome.

The relationships between physiology and behaviour of juvenile *A. polyacanthus* were dependent on developmental environmental conditions. Often it is expected that individuals with greater resting metabolic rate (oxygen consumption as a proxy) and aerobic scope have a greater capacity for bold and highly active behaviours (Biro and Stamps, 2010; Metcalfe et al., 2016). Counter to this expectation, we found that the reduced resting oxygen consumption observed in elevated CO_2 is likely to be driven by the plasticity of shy individuals (Biro and Stamps, 2010; Metcalfe et al., 2016). Laubenstein et al. (2019) also found no clear relationship between aerobic capacity and behaviour measured in terms of an anti-predator response, until juvenile *A. polyacanthus* were reared under warm temperature and elevated CO_2 combined. In this case, individuals with a lower antipredator response had a higher aerobic scope under combined stressor conditions (Laubenstein et al., 2019). This may indicate that a greater aerobic capacity is beneficial for defensive behaviours, such as anti-predator response, compared to exploratory behaviours as tested in our experiment (Metcalfe et al., 2016). In any case, boldness is not considered to be without risks and costs and while it can increase access to resources it can also increase the risk of predation (Nash and Geffen, 2012).

The transfer of an enhanced condition or greater standard length through carry-over effects can be adaptive in nature as it enhances offspring performance regardless of the offspring environment and therefore does not require complex machinery to assess environmental conditions (Jablonka et al., 1995; Bonduriansky and Crean, 2018). Juveniles from both grandparental thermal exposures were larger than the control cross-generation, regardless of juvenile developmental treatment. These results suggest that prior exposure to warm temperatures in the grandparental generation during development was beneficial, resulting in longer fish within the F_3 generation. However, juveniles from grandparents with developmental exposure had lower survival in both temperatures under ambient CO_2 conditions. In combination, this indicates that all transgenerational effects were not simply induced by the early development conditions of grandparents, and the nature of conditions experienced by previous generations can make predicting plasticity across generations in response to environmental change challenging. Interestingly, juveniles from parents developmentally exposed tended to be in better condition than those from grandparents developmentally exposed and were not different in standard length across all developmental treatments (Jablonka et al., 1995; Bonduriansky and Crean, 2018). In contrast, Spinks et al. (2022) found negative carry-over effects in the previous generation whereby prior exposure to warming in the F_1 generation decreased offspring length and condition in the F_2 generation across all offspring developmental temperatures. Both lower body size (Pörtner and Knust, 2007; Forster et al., 2012; Leiva et al., 2019) and increased physical condition (Robinson et al., 2008) has been found to correlate with improved thermal tolerance of aquatic organisms. Therefore, the variation in which a morphological trait is selected for and subsequently carried over to the next generation can stem from differences in the micro-environments such as diurnal temperature fluctuations, metabolic costs, or other intrinsic factors (Bonduriansky and Crean, 2018). These various factors play a crucial role in shaping evolutionary outcomes and the adaptive responses of organisms within their specific habitats.

Evidence for transgenerational plasticity was also found with enhanced aerobic performance by juveniles from grandparents continuously exposed to warming and that developed at warm temperature and control CO_2. However, it was not significantly different to other cross-generational experiences within the same juvenile developmental treatment. Our findings were dissimilar to Bernal et al. (2022), where grandparental exposure to warming (+1.5 °C) resulted in increased aerobic scope in both control and +1.5 °C juvenile developmental temperatures. This may represent experimental differences and the conditions in which the F_3 embryos develop, with Bernal et al. (2022) fish experiencing embryogenesis at +1.5 °C and the present study developing in control. Unexpectedly, the enhanced aerobic capacity produced by grandparents continuously exposed to warming did not also occur in juveniles that developed at warm temperature with CO_2 exposure. One possible explanation is that elevated CO_2 induced developmental physiological plasticity that reduced resting metabolic rate, and this outweighed any transgenerational plasticity on maximum metabolic rate or aerobic scope (Shama and Wegner, 2014; Burggren, 2015). Individuals and species with higher maximum metabolic rate and aerobic capacity tend to have a higher standard metabolic rate (and hence resting metabolic rate) to support the required physiological machinery (Biro and Stamps, 2010; Killen et al., 2016; Metcalfe et al., 2016). This pattern highlights the importance of directly testing plastic outcomes in a range of conditions as phenotypic outcome are context dependent with transgenerational plasticity.

By reflecting on the cross-generational experiences that produce carry-over effects and transgenerational plasticity in this study we aim to better understand the circumstances under which various types of plasticity occur (Reed et al., 2010; Herman et al., 2014; Leimar and McNamara, 2015). The fact that transgenerational plasticity in aerobic performance only occurred when grandparents and juveniles were exposed to the same conditions, is in line with the theory that transgenerational plasticity will manifest when conditions are changing predictability between generations (Salinas et al., 2013; Donelson et al., 2018). The only other evidence of transgenerational plasticity was observed in poorer survival of offspring from developmental grandparents in present day control versus elevated CO_2 conditions. Yet, these same thermal exposure periods within grandparent and parent generations resulted in positive carry-over effects in standard length. Our experimental design endeavours to focus on non-genetic plasticity rather than genetic selection, however, it is possible that some differences are due to the genetics of which F_2 fish reproduced. If non-genetic in nature, rather than selection, these carry-over effects may arise from a range of mechanisms including the transfer and inheritance of non-genetic epigenetic cues (DNA methylation), hormones, or nutritional resources (Jablonka et al., 1995; Bonduriansky and Day, 2009; Miller et al., 2012). Regardless of the mechanism, the phenotype of a larger body size is expected to be beneficial under all environmental conditions (Sogard, 1997) and perhaps any costs of production are outweighed by benefits. Much of the previous work on this species has also found predominantly carry-over effects (Donelson et al., 2012a; Welch et al., 2014; Spinks et al., 2022), which aligns with theoretical expectations on the basis that this tropical species broods its offspring, and environmental conditions across years and generations is likely to be predictable (Harrison et al., 2011).

4.1. Conclusion

Due to the complex nature of marine environments, multiple stressor experiments are important for determining if unpredictable interactions occur compared to single stressors alone. This research takes a novel step forward and shows that the impact of elevated CO_2 did not differ depending on whether previous generations experienced ocean warming. This meant that potential benefits of historical thermal plasticity were generally realised regardless of elevated CO_2 conditions, but equally, any likely beneficial (reduced resting metabolic rate), or negative effects (reduced length), also remained. The lack of interaction between ocean warming and acidification within a generation observed on the performance traits measured in this study matches much of the previous research showing additive responses (Munday et al., 2009a; Miller et al., 2012; Lefevre, 2016). Additive effects mean a relatively predictable extrapolation of the future impacts of multiple stressors from single stressor experiments (Lefevre, 2016; McMahon et al., 2019). Overall, the largest diversity of F_3 juvenile traits were influenced by developmental temperature implying that the thermal environment experienced in early life has a greater influence on juvenile phenotype than that of previous generations. These findings are critical for forecasting how site-attached tropical reef species, already close to their thermal maximum, will cope with the mounting pressures of climate change across future generations.

CRediT authorship contribution statement

Jasmine S. Cane: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yogi C. Yasutake:** Writing – review & editing, Investigation. **Shannon J. McMahon:** Writing – review & editing, Methodology, Conceptualization. **Andrew S. Hoey:** Writing – review & editing, Supervision. **Jennifer M. Donelson:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Ethical approval

This project followed James Cook University animal ethics guidelines (JCU Animal Ethics No. A2800).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was funded by the Australian Research Council [FT190100015, JMD], the ARC Centre of Excellence for Coral Reef Studies, Australia [JSC, JMD], and support from the College of Science and Engineering, James Cook University, Australia. We thank Ben Lawes, Simon Wever, Nathan Cleasby, and Jarrod Guppy at the Marine and Aquaculture Facility Unit at James Cook University for their invaluable aquaculture technical support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107451.

Data availability

The data is available on research data Australia (https://doi.org/10.25903/mcks-t205).

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