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Thermal history influences reproduction but not offspring quality in a coral reef fish

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ABSTRACT: Tropical reef fish are especially sensitive to ocean warming, and the impacts of warming on reproduction may influence the persistence of future populations. The capacity of phenotypes to match altered conditions depends on the nature of environmental change, such as timing, duration, and variability. However, little is known about how these characteristics alter the plasticity of reproduction. The present study investigated how the timing of warming (+1.5°C above present-day temperature) through early development (hatching—1.5 yr) and/or post-maturation (1.5—3 yr) impacted reproduction and offspring quality in a tropical damselfish (*Acanthochromis polyacanthus*). Warming at both life stages affected adult morphometrics and reproduction differently, but offspring quality was not impacted by parental thermal experience. Specifically, warming during development resulted in smaller adults (shorter standard lengths) with significantly reduced fecundity, while warming after maturation led to lighter adults for a given length that produced smaller eggs. This study also highlighted that fish may be able to partially restore their reproductive output in elevated temperatures with extended experience of warming after maturation. However, negative impacts from developing in elevated temperatures remained even in their second breeding season when fish were 3 yr old. Such knowledge of how aspects of temperature change influence environmental sensitivity and the capacity for plasticity is important to understand the drivers of species' resilience to change.

KEY WORDS: Global warming · Phenotypic plasticity · Acclimation · Marine fish · Temperature · Breeding performance · Development · Climate change

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1. INTRODUCTION

The biological impact of environmental change depends on the sensitivity of organisms and their inherent capacity to cope with change. Having evolved in a stable thermal environment, tropical ectotherms are expected to be particularly sensitive to warming as their physiology is tuned to narrow temperature ranges (Stillman 2003, Deutsch et al. 2008, Tewksbury et al. 2008). Thus, their persistence may be affected if phenotypic plasticity and/or genetic adaptation of thermal performance does not keep up with the rate of environmental change. Genetic adaptation alone is expected to be insufficient to keep pace with the current rate of climate change (Munday et al. 2013, Crozier & Hutchings 2014), even for species with short generation times (e.g. zebrafish; Morgan et al. 2020). Acclimation through phenotypic plasticity may consequently be important in providing rapid resilience, affording time for genetic adaptation to occur (Chevin et al. 2010, Grenier et al. 2016, Fox et al. 2019, Sandoval-Castillo et al. 2020).

One aspect of thermal plasticity research that requires further investigation is how various compo-

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nents of environmental experience, within and across generations, influence phenotypic outcomes. Thermal sensitivity and plastic capacity of traits may be affected by aspects of environmental change, such as the timing, duration, predictability, and magnitude (Angilletta 2009, Reed et al. 2010, Uller et al. 2013, Snell-Rood et al. 2015, Le Roy et al. 2017, Donelson et al. 2018). In particular, early life (Truebano et al. 2018, Pandori & Sorte 2021) and reproduction (Pankhurst & Munday 2011) are 2 thermally sensitive life stages, while also being important for producing phenotypic responses in subsequent life stages and future generations (West-Eberhard 2003, Burton & Metcalfe 2014, Burggren & Mueller 2015, Fawcett & Frankenhuis 2015). In addition, phenotypic plasticity is most likely to be adaptive when individuals can accurately predict subsequent environmental conditions (Lande 2009, Reed et al. 2010). As environmental heterogeneity across time and space is projected to increase with warming (Meehl & Tebaldi 2004, Rahmstorf & Coumou 2011, Rummukainen 2012), phenotypic responses and their benefits may be altered in the future (Burgess & Marshall 2014, Herman et al. 2014, Leimar & McNamara 2015).

Successful reproduction is fundamental for populations to persist. However, reproductive processes are often highly sensitive to warming (Van Der Kraak & Pankhurst 1997, Pankhurst & King 2010), and spawning individuals are required to meet additional energy requirements for gamete production and increased biomass (Pörtner & Farrell 2008, Pörtner & Peck 2010). As such, thermal conditions during spawning may represent a bottleneck for the completion of life cycles in fish (Dahlke et al. 2020, McKenzie et al. 2021). Successful reproduction depends on a series of events from early development through to spawning (e.g. gonadal differentiation, gametogenesis, gamete maturation) (Lema et al. 2024), and impacts of environmental temperature are expected to vary depending on when warming is experienced relative to these events. For example, warming during development can influence processes of sex determination and maturation in fish, commonly leading to masculinization (Ospina-Álvarez & Piferrer 2008, Geffroy & Wedekind 2020, Kitano et al. 2024) and advancement of sexual maturation (Kuparinen et al. 2011, Loisel et al. 2019). Temperature during development could also indirectly impact reproduction whereby poorer juvenile growth (Taborsky 2006) leads to smaller adults with reduced fecundity (Barneche et al. 2018). In contrast, thermal impacts at spawning depend on whether temperature exceeds thermal limits for gamete production and maturation (Alix et al. 2020, Servili et al. 2020, Zahangir et al. 2022). Warming beyond the optimum could inhibit spawning altogether (Soria et al. 2008, Vikingstad et al. 2016) or reduce the quantity or quality of the gametes produced (Pankhurst & Munday 2011, Foo & Byrne 2017). Although shifts in phenology and/or spawning location may allow reproduction to occur at optimal temperatures (Crozier & Hutchings 2014, Ciannelli et al. 2015), this may compromise offspring survival due to suboptimal developmental conditions (Barlow et al. 1995, Stenseth & Mysterud 2002, Shoji et al. 2011). Consequently, phenotypic shifts in the thermal sensitivity of reproduction may be especially important (Rummer & Munday 2017, Lema et al. 2024), as they allow reproductive performance and offspring viability to be maintained in warming environments.

The influence of developmental (reviewed in Vagner et al. 2019, Jonsson et al. 2022, Pottier et al. 2022) or parental (reviewed in Salinas et al. 2013, Donelson et al. 2018) temperature on subsequent performance has been documented in an array of traits in fish (e.g. growth, aerobic metabolism, thermal tolerance). However, despite reproductive success being a direct measure of fitness, how prior temperature experience shapes the thermal performance of reproduction in fish has rarely been tested. Studies to date suggest some capacity to mitigate the impacts of warming on reproduction through developmental plasticity (Donelson et al. 2014, Fuxjäger et al. 2019, Spinks et al. 2021), with improved capacity when warming is experienced across generations (Donelson et al. 2016). In most studies, however, parents have been consistently exposed to warming after hatching to reproduction (but see Spinks et al. 2021), limiting our understanding of how specific life stages (e.g. during development or after maturation) drive plasticity within an individual's lifetime. Furthermore, to our knowledge, no experimental study to date has investigated warming impacts on reproduction beyond the first breeding season, and whether adults can acclimate their reproductive performance at elevated temperatures across years is less known.

The present study investigated how temperature during development (hatching to maturity: 0–1.5 yr) and post-maturation (1.5–3 yr) influences the capacity for plasticity of reproduction in the damselfish *Acanthochromis polyacanthus*. This is one of the first studies on tropical fish to incorporate both seasonal and daily changes in temperature to account for influences of thermal variability on phenotypic responses (Reed et al. 2010, Vasseur et al. 2014, Burton et al. 2020, Schunter et al. 2021). It builds on previous research conducted on the same group of fish, exploring sex- and time-specific effects of warming on reproduction and offspring quality (Spinks et al. 2021). Specifically, adult fish used in Spinks et al. (2021) were exposed to their post-maturation treatments for an additional year (making a total of 1.5 yr at their post-maturation treatments) to investigate how thermal sensitivity is influenced by a longer experience of warming after maturation. Using a fully orthogonal design, this study investigates how ontogenetic timing (development versus post-maturation) and the extended duration of warming influence reproduction and offspring quality in *A. polyacanthus*.

2. MATERIALS AND METHODS

2.1. Study species and experimental design

The spiny chromis *Acanthochromis polyacanthus* (Bleeker 1855) is a tropical damselfish widely distributed across the Indo-Pacific (15° N–26° S, 116–169° E). *A. polyacanthus* form size-assortative monogamous breeding pairs, with peak reproduction between late austral spring and early summer when the water temperature is typically between 27 and 29°C (Thresher 1983). Both parents provide care to the benthic eggs and developing offspring for 1–2 mo (Pankhurst et al. 1999, Kavanagh 2000). Females exhibit group synchronous ovarian development and can produce multiple clutches in a single breeding season (Pankhurst et al. 1999).

Briefly, 6 wild pairs (F_0, Families A–F) 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 July 2015. These F_0 fish were transported to the Marine and Aquaculture Research Facility at James Cook University, Townsville, and maintained under seasonally fluctuating temperatures typically seen in these inshore collection locations (see Spinks et al. 2021 for more details). F_0 pairs produced clutches between February and March 2016 at the usual summer water temperatures for the collection region (28.5°C). These juveniles (F_1) were split randomly at hatching into 2 temperature treatments: present-day (control) and elevated (warm: +1.5°C) temperatures. Average warming of +1.5°C already occurs during marine heatwaves (Frölicher et al. 2018) and was chosen to reflect moderate warming projected to occur in the Great Barrier Reef by 2050–2100 (Collins et al. 2013). This also allows direct comparison with previous research on reproduction in *A. polyacanthus* (Donelson et al. 2010, 2014, 2016, Spinks et al. 2021). The present-day water temperature was simulated on seasonal (winter: 23.2°C; summer: 28.5°C) and diurnal (±0.6°C) cycles for the Palm Island region based on temperature loggers from 2002 to 2015 at 0.2–14.6 m depth (Australian Institute of Marine Science 2017), with the elevated treatment following the same pattern but 1.5°C warmer (24.7–30°C; Spinks et al. 2021). Photoperiod also replicated the natural cycle for the collection location, with adjustments made weekly. Water quality was maintained with mechanical, biological, and ultraviolet filtration, protein skimming, and partial water changes.

F_1 juveniles were maintained in family groups throughout development until they reached reproductive maturity at approximately 1.5 yr. At hatching, juveniles from each F_0 family lineage were divided among multiple replicate tanks (42 l) for each developmental treatment: control (Family A: 10; B: 8; C: 9; D: 9; E: 5; F: 5 tanks) and warm (Family A: 10; B: 14; C: 9; D: 9; E: 5; F: 5 tanks). Each replicate tank housed approximately 10 newly hatched juveniles, with density adjusted over time to account for growth and competitive interactions (see Spinks et al. 2021 for details). At 8 mo, fish were sexed by visually inspecting their gonads and subsequently tagged with elastomers to identify their treatment, sex, and family. At 1 yr, tank density was reduced to sibling pairs to minimise competitive fighting. During this developmental period, water temperature was controlled using 4 internal sumps: 2 for control and 2 for warm treatments. At 1.5 yr, when this species reaches reproductive maturity, fish were transferred to a separate aquarium room and orthogonally organised into non-sibling pairs under 2 post-maturation treatments: control (22 pairs) and warm (21 pairs). Water temperature after maturation was controlled using 6 internal sumps: 3 for control and 3 for warm.

The present study used breeding pairs comprising a male and a female fish maintained at the same developmental and post-maturation temperatures, resulting in 4 treatments: (1) developmental control and post-maturation control (control–control); (2) developmental control and post-maturation warm (control–warm); (3) developmental warm and post-maturation control (warm–control); and (4) developmental warm and post-maturation warm (warm–warm) (Fig. 1). The strength of this design is that it separates the effects of developmental and post-maturation reproductive temperatures, allowing us to investigate how these exposure timeframes (both in isolation and with interaction) influence reproduction in the second breeding season. While the fish used in the present study overlap with fish from Spinks et al. (2021), adult fish were allocated

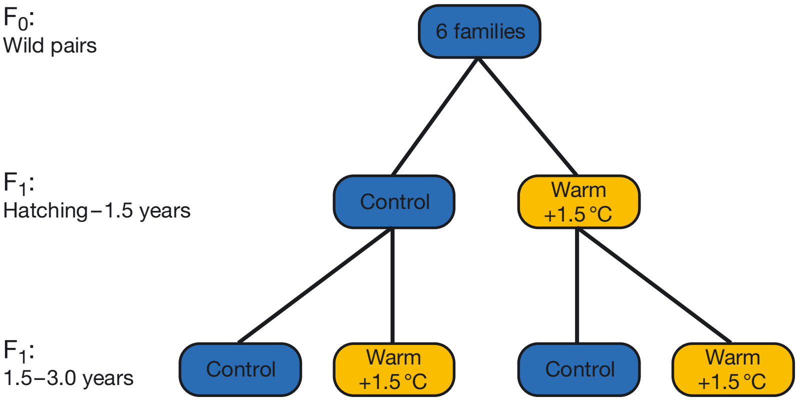

Fig. 1. Experimental design to investigate thermal impacts during development and/or post-maturation in *Acanthochromis polyacanthus*. Blue boxes: present-day temperature treatment (control); yellow boxes: elevated temperature treatment (warm; +1.5°C)

a new partner of similar size (as they prefer) from the same treatment in September 2018, when water temperatures were slowly increased from winter to summer (August–November: 0.2–0.5°C wk^{-1}). Pairs were distributed across the 4 treatments (control–control: 13 pairs; control–warm: 13 pairs; warm–control: 9 pairs; warm–warm: 8 pairs), with a maximum of 3 replicate tanks for a given treatment × female family × male family combination (Table S1 in the Supplement at www.int-res.com/articles/suppl/m756p095_supp.pdf).

Fish were fed live *Artemia* nauplii upon hatching and then weaned to commercial pellets of different sizes depending on their age (Appendix S1 in Spinks et al. 2021). During the summer breeding seasons, adults were fed twice daily, representing ~0.4 g of food per adult (1.3% of body mass per day).

2.2. Reproduction and offspring sampling

Nesting sites of F_1 breeding pairs were checked daily (~08:00 h) for the presence of eggs. When a clutch had been laid, an underwater photo was taken to count the number of eggs using an image processing program (ImageJ, Fiji, v.2.0.0-rc-69/1.53c) (Schindelin et al. 2012). Depending on the clutch, 9–10 eggs were collected from random locations to minimise the potential impacts of egg positioning. Egg samples were then preserved with ~6% formalin dissolved in seawater as per Donelson et al. (2008). Egg size (mm^2) was calculated using the area function of ImageJ with a macro photograph of samples taken on 5 × 5 mm grids. As some breeding pairs only produced a single clutch, egg size and clutch size were compared using only the first clutch produced by each pair. In contrast, reproductive performance across the breeding season was investigated using the total number of clutches and total eggs produced by each pair throughout the season. Due to other experiments being conducted on the offspring beyond this study, offspring were removed from the care of parents on the day of hatching. This allowed pairs to produce more clutches than would happen in nature. Consequently, data beyond the third clutch were excluded, as it is expected that wild pairs produce no more than 3 clutches in a breeding season (Robertson 1973, Pankhurst et al. 1999). The scale of inference for reproductive (and juvenile) traits was confined to numbers of breeding pairs that successfully produced a clutch (control–control: 6; control–warm: 6; warm–control: 5; and warm–warm: 3). A total of 60 (control–control), 59 (control–warm), 50 (warm–control), and 30 (warm–warm) eggs were sampled to assess thermal impacts on egg size.

Embryonic development took from 9 to 12 d, depending on water temperature, with hatching generally occurring mid-day as is usual for this species. Depending on the clutch size, 12–21 juveniles were collected at hatching for morphological measurements. This was to ensure that sufficient juveniles were available to be grown out for a separate study investigating the impacts of parental thermal experience on juveniles. Fish were euthanized with an overdose of clove oil in seawater before being fixed in 10% neutral buffered formalin. Weight (*W*), standard length (SL) and yolk area (YA) were measured after fixation following previous protocols (Donelson et al. 2008, 2012, 2014), which have been found to cause negligible shrinkage (Donelson et al. 2008). *W* was measured to the closest 0.1 mg after the fish were blotted dry, while SL and YA were measured to the nearest 0.001 mm with ImageJ using photos of hatchlings taken on 5 × 5 mm grids (Donelson et al. 2012). Juvenile condition was calculated as *W* for a given SL (condition; e.g. Lai & Helser 2004, Ma et al. 2017). A total of 112 (control–control), 120 (control–warm), 94 (warm–control), and 61 (warm–warm) newly hatched juveniles were sampled to investigate thermal impacts on offspring quality. One newly hatched juvenile from warm–warm was excluded from the analysis on weight and condition due to a measurement error for weight.

Following the summer breeding season in April 2019, all F_1 adults were anesthetized using clove oil and seawater to measure their SL (to the closest

0.01 mm) and W (to the closest 0.01 g). Proxies for physical condition were calculated using both Fulton's K equation (FK = 100 × $W\,\text{SL}^{-3}$) as well as condition. Adults recovered in aerated containers before being returned to their respective tanks. A total of 26 (control—control), 26 (control—warm), 18 (warm—control), and 16 (warm—warm) F_1 adults were measured to investigate thermal impacts on adult morphometrics.

2.3. Statistical analysis

The influence of temperature treatments (developmental temperature, post-maturation temperature, and their interaction: fixed factor) on physical variables of F_1 adults (SL, W, condition) was analysed using linear mixed-effects models (LMMs), with family lineage (Families A—F) included as random factors (Tables S2 & S3). Specifically, thermal impact on condition (i.e. weight for a given length) was analysed using W as a response variable and SL as a covariate. Models were also constructed including the gender of F_1 adults as a covariate to determine whether the morphometrics of males and females were differentially influenced by their thermal history. Gender had no significant influence on adult morphometric traits (SL, W, and condition) and was consequently excluded from the final model based on Akaike's information criterion (AIC) values. In addition to condition, we tested FK (Table S2, Fig. S1) to corroborate whether the results were similar and to allow FK to be used as a covariate where appropriate (e.g. see egg size below).

The effect of thermal treatments (developmental treatment, post-maturation treatment, and their interaction: fixed factor) on reproductive variables was analysed using generalized linear mixed-effects models for count data (number of clutches per pair, clutch size, and total eggs per pair) and LMMs for egg size (Tables S4 & S5). The appropriate error structure for count data (Poisson or negative binomial) was selected based on a dispersion test. A Poisson error structure was selected for the number of clutches per pair, while negative binomial was chosen for clutch size and total eggs per pair. For egg size, a random factor of F_1 female ID nested within sump (i.e. the scale of temperature manipulation) was included to capture variations among breeding pairs (e.g. differences among individual females and their male partners, and their F_0 family lineage) and among tanks within the same sump (e.g. temperature differences due to tank position or water flow) (Tables S4b & S5b).

The correlation between reproductive performance and maternal physical variables (SL, W and FK) was explored with simple linear regression to incorporate maternal effects. Maternal SL and FK were significantly correlated with clutch size (larger females produced larger clutches; adjusted $r^2 = 0.276$, $F_{1,18} = 8.22$, $p = 0.010$) and egg size (females in better condition produced larger eggs; adjusted $r^2 = 0.218$, $F_{1,18} = 6.30$, $p = 0.022$), respectively. These maternal variables were included in the final model if they improved fit based on AIC values; maternal SL was included for clutch size, while maternal FK was excluded for egg size (see Table S6 for outputs including maternal FK for egg size). Finally, the proportion of pairs that reproduced was compared across temperature treatments using Pearson's chi-squared test to investigate whether temperature experience influenced the occurrence of breeding.

The effect of parental thermal treatment (developmental temperature, post-maturation temperature, and their interaction: fixed factor) on offspring quality at hatching (SL, W, YA, and condition) were explored with LMMs (Tables S7 & S8). As with egg size, a random factor of F_1 female ID nested within sump was included to account for variability across breeding pairs and tanks. For condition, SL and W were both $\log_{10}$ transformed to adhere to the assumptions of linearity (Froese 2006). As with reproductive traits, maternal effects on offspring variables were also explored, but no maternal traits (SL, W, and FK) showed a significant correlation with offspring. In addition, the correlation between offspring variables and average egg size was explored. Average egg size was positively correlated with juvenile SL (adjusted $r^2 = 0.311$, $F_{1,18} = 9.58$, $p = 0.006$) and YA (adjusted $r^2 = 0.322$, $F_{1,18} = 10.02$, $p = 0.005$) (see Table S9 for model outputs including egg size as a covariate).

Following the construction of models, main effects were determined using a Type II Wald chi-squared test for count data, and a Type III sequential F-test with Satterthwaite's approximation for normally distributed data ($\alpha = 0.05$ for both tests). All analyses were performed using R (v.4.1.10) (R Core Team 2021) and the associated packages 'car' (Fox & Weisberg 2019), 'DHARMa' (Hartig 2024), 'dplyr' (Wickham et al. 2023), 'emmeans' (Lenth 2024), 'ggplot2' (Wickham 2016), 'ggpubr' (Kassambara 2023), 'glmmTMB' (Brooks et al. 2017), 'gridExtra' (Auguie 2017), 'lme4' (Bates et al. 2015), 'lmerTest' (Kuznetsova et al. 2017), 'MASS' (Venables & Ripley 2002), 'MuMIn' (Bartoń 2023), 'nlme' (Pinheiro et al. 2023), 'patchwork' (Pedersen 2020), 'plyr' (Wickham 2011), 'readxl' (Wickham & Bryan 2023), 'sjplot' (Lüdecke 2023), and 'vegan' (Oksanen et al. 2022).

3. RESULTS

3.1. F_1 adult morphometrics

Adults that developed at an elevated temperature were on average 3.3% shorter in SL (ANOVA: $F_{1,78}$ = 6.76, p = 0.011; Fig. 2a), and tended to be 7.2% lighter ($F_{1,78}$ = 3.37, p = 0.070; Fig. 2b) than fish from the developmental control treatment. In contrast, adults in the post-maturation warm treatment were 4.2% lighter for a given length ($F_{1,77}$ = 5.49, p = 0.022; Fig. 2c) than adults in post-maturation control. Although the interaction between developmental and post-maturation treatment had a marginal effect on adult SL ($F_{1,78}$ = 3.85, p = 0.053; Fig. 2a), no adult physical attributes (SL, *W*, condition) were significantly influenced by this interaction (Table S2). Specifically, at post-maturation control, adults had similar SL (~8.93 cm) irrespective of their developmental temperature. In contrast, at post-maturation warm, adults that developed in the warm treatment were on average 5.7% shorter than those that developed in the control.

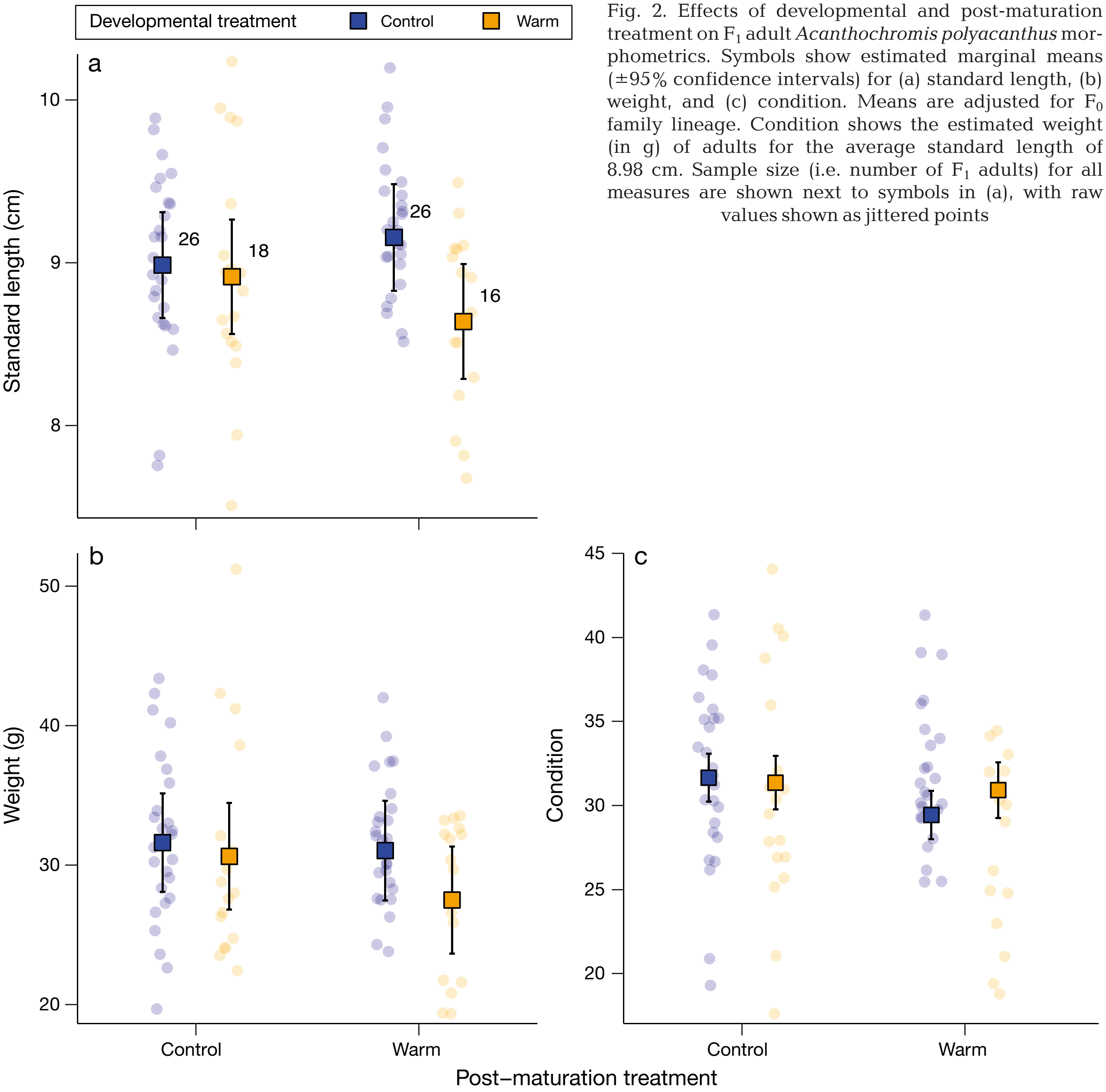

Fig. 2. Effects of developmental and post-maturation treatment on F_1 adult *Acanthochromis polyacanthus* morphometrics. Symbols show estimated marginal means (±95% confidence intervals) for (a) standard length, (b) weight, and (c) condition. Means are adjusted for F_0 family lineage. Condition shows the estimated weight (in g) of adults for the average standard length of 8.98 cm. Sample size (i.e. number of F_1 adults) for all measures are shown next to symbols in (a), with raw values shown as jittered points

3.2. Reproductive performance

A similar proportion of pairs reproduced across all development and post-maturation treatment combinations (Pearson's chi-squared test: $\chi^2 = 0.558$, df = 3, p = 0.906), with reproductive success ranging between 37.5 and 63% across treatments. Developmental temperature significantly influenced fecundity, with pairs that developed in the control treatment producing ~8600 eggs across the breeding season (control—control pairs: 4344 eggs; control—warm pairs: 4289 eggs) compared to ~3550 eggs from pairs that developed at warm temperatures (warm—control pairs: 2192 eggs; warm—warm pairs: 1355 eggs). Although pairs produced similar numbers of clutches (Table S4a, Fig. 3a) of comparable size (Table S4a, Fig. 3b) across developmental treatments, pairs at developmental control temperatures produced ~300 more eggs over

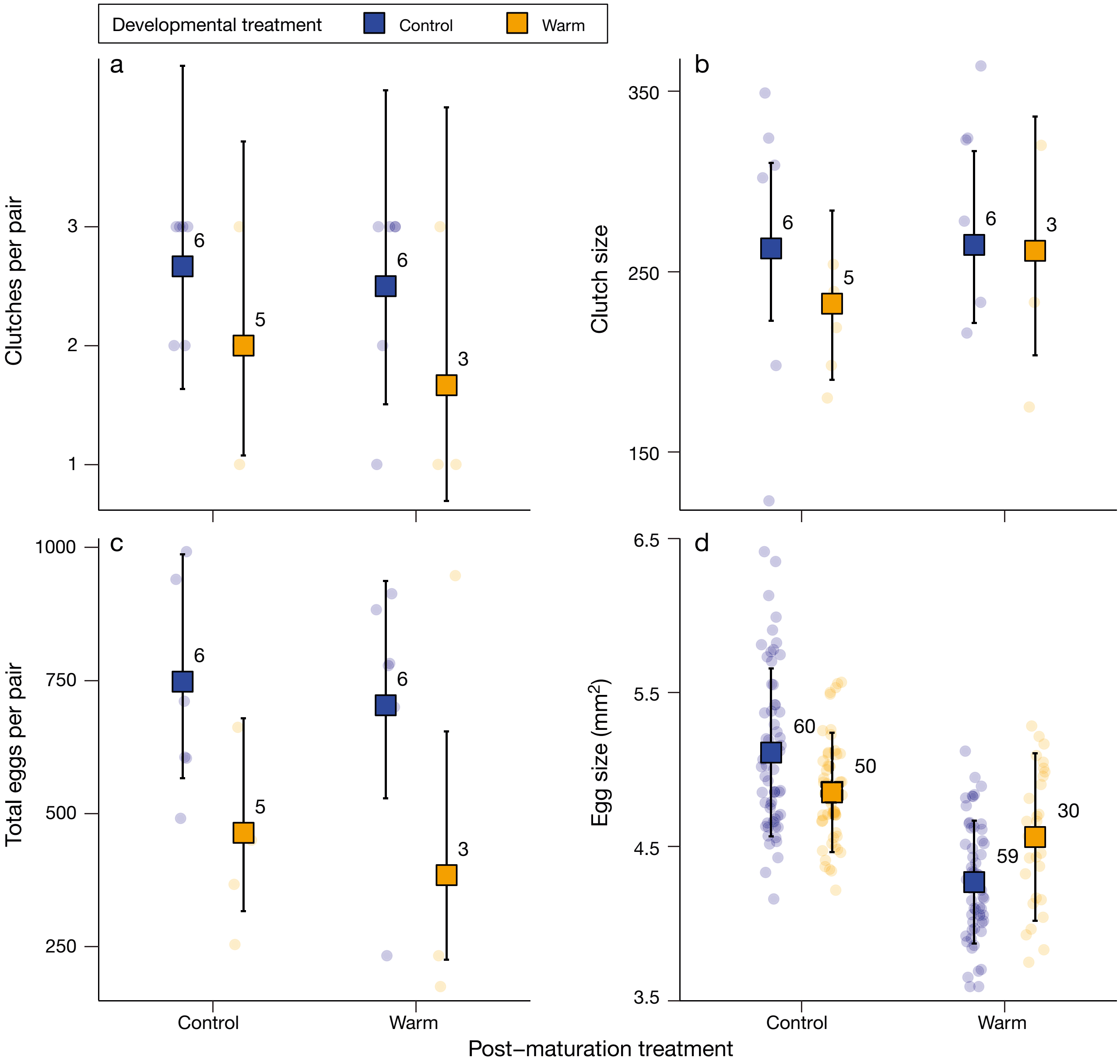

Fig. 3. Effects of developmental and post-maturation temperature on reproductive performance in *Acanthochromis polyacanthus*. Symbols show estimated marginal means (±95% confidence intervals) for (a) number of clutches per pair, (b) clutch size, (c) total eggs per pair, and (d) egg size. Clutch sizes are adjusted for the covariate of female length, and egg size is adjusted for the random factor of female ID nested within sump. Number of breeding pairs (a—c) or eggs (d) are given next to symbols, with raw values shown as jittered points

the breeding season (Type II Wald chi-squared test: $\chi^2 = 7.809$, $p = 0.005$; Fig. 3c), driving the higher total egg output at developmental control. Developmental temperature, however, did not influence egg size (Table S4b).

In contrast, warming after maturation resulted in pairs producing smaller eggs (~11.4%) than those at post-maturation control (Type III sequential *F*-test: $F_{1,16} = 10.53$, $p = 0.005$; Fig. 3d). No reproductive traits (egg size, clutch size, number of clutches per pair, and total eggs per pair) were impacted by the interaction between developmental and post-maturation treatments (Table S4). Aspects of reproductive performance were also influenced by maternal morphometrics irrespective of thermal treatments. Specifically, larger ($r^2 = 0.276$, $F_{1,18} = 8.224$, $p = 0.010$) or heavier ($r^2 = 0.232$, $F_{1,18} = 5.422$, $p = 0.032$) females produced larger clutches, and females with higher FK produced larger eggs ($r^2 = 0.218$, $F_{1,18} = 6.23$, $p = 0.022$).

3.3. Offspring at hatching

Offspring morphology at hatching (SL, *W*, YA, and condition) was not significantly impacted by the thermal experience of parents (Table S7), despite the observed impacts on reproduction. While not significant, juveniles produced by parents that experienced both development and post-maturation warm temperatures were approximately 0.12–0.20 mm shorter than offspring from all other parental treatments (Fig. 4a). Juveniles from parents that developed at warm temperatures tended to be 0.26 mg heavier (Fig. 4b), and 7.6% heavier for a given length (Fig. 4c) than those from parents that developed at control temperatures (not significant; Table S7), while those produced at post-maturation warm tended to possess 6.7% less yolk reserve (Fig. 4d) than those produced at post-maturation control (not significant; Table S7). Offspring length and yolk size at hatching, however, were influenced by egg size irrespective of thermal treatments, where juveniles from larger eggs were longer ($F_{1,15} = 9.37$, $p = 0.008$; Table S9a) and possessed more yolk reserve ($F_{1,15} = 7.05$, $p = 0.018$; Table S9a).

4. DISCUSSION

Accurately representing the relationship between environmental experience and biological response is essential for predicting the persistence of species in a warmer future. Our study highlighted the long-lasting impacts of developmental conditions, as warming resulted in smaller adults that produced ~60% fewer eggs compared to adults that developed in the present-day temperature. In contrast, warming after maturation led to adults being lighter for a given length and producing smaller eggs. Interestingly, however, these negative impacts of warming did not carry over to influence offspring traits at hatching. In addition, the impacts of post-maturation warming on fecundity were partially mitigated across breeding seasons with an extra year at elevated temperature, highlighting some capacity for reproductive plasticity within a generation. Contrary to previous research, however, the present study found limited evidence for developmental plasticity. This is possibly due to our study simulating more realistic future scenarios, including diurnal temperature fluctuations and investigating breeding beyond the first season of maturity. Our results highlight that predicting the effects of ocean warming on marine fish is complex, as various aspects of reproduction are influenced depending on the timing, duration, and variability of the thermal experience.

The effects of temperature on adult physical variables depended on when warming was experienced. Most notably, warming during development resulted in smaller adults, while warming after maturation led to adults being lighter for a given length. Generally, warming towards the thermal optimum for growth is expected to increase body size if sufficient food is available to sustain higher metabolic rates at elevated temperatures (Jobling 1997). As such, a small increase within natural temperature ranges can improve the growth rates of tropical reef fish larvae (Meekan et al. 2003, Green & Fisher 2004, Sponaugle et al. 2006), often enhancing their survivorship to recruitment (Bergenius et al. 2002, Wilson & Meekan 2002). In accordance with other experimental studies documenting reduced juvenile and adult growth with developmental warming (Munday et al. 2008, Donelson et al. 2011, Rodgers et al. 2017), the present study suggests that 1.5°C above present-day temperatures may be beyond the thermal optimum for growth for *Acanthochromis polyacanthus*. The observed reduction in growth may be partly due to energetic trade-offs from increased metabolic rate (Nilsson et al. 2009, Gardiner et al. 2010, Rummer et al. 2014). However, in such a case, we would expect warm–control fish to have caught up to control–control fish, as the rations used in the present study represent high feeding levels for *A. polyacanthus* (1–2% of their body mass; Donelson et al. 2010). Thus, it is likely that the observed reduction in growth may represent a cost of

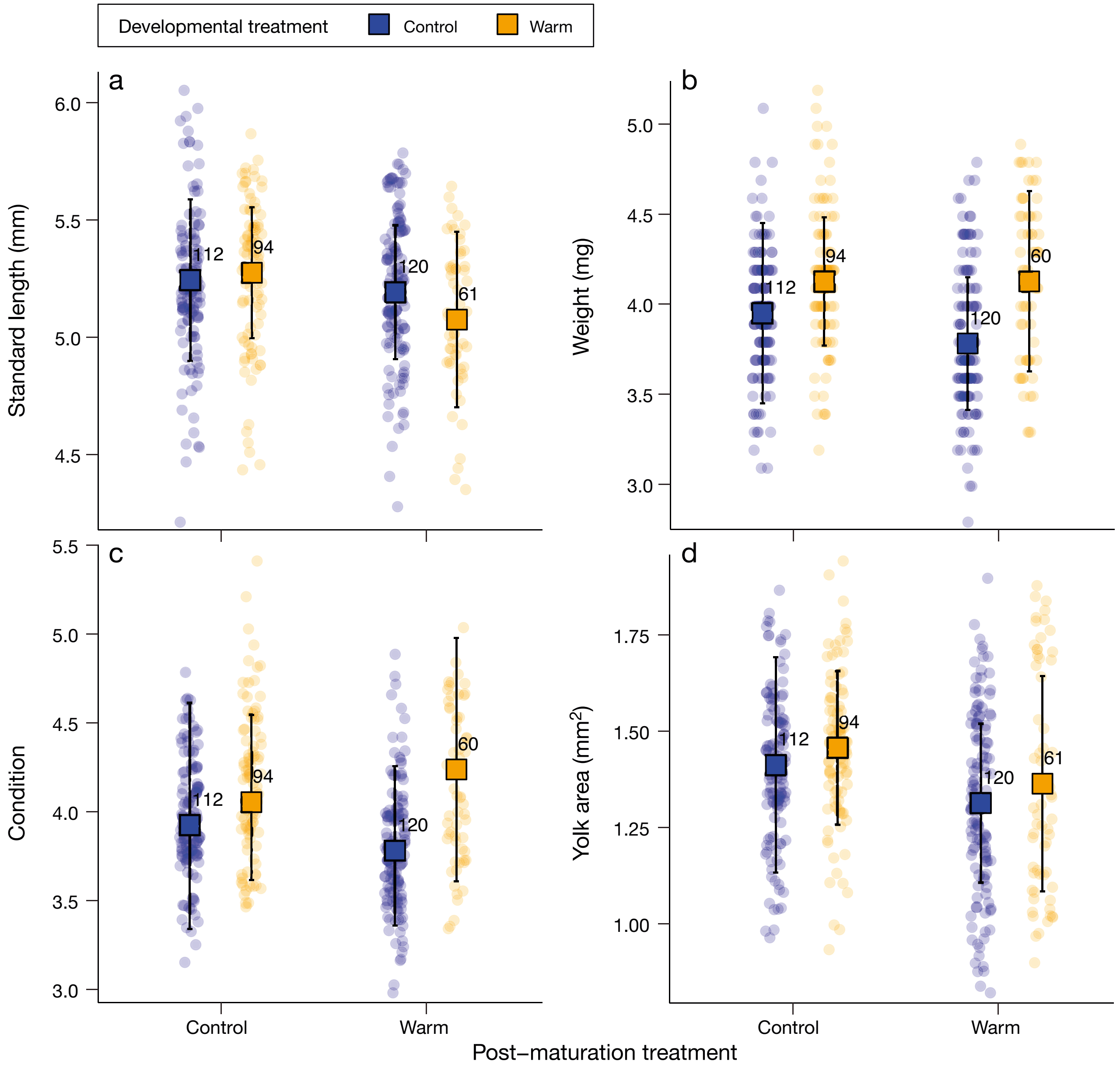

Fig. 4. Effects of F_1 development and post-maturation temperature on F_2 juvenile *Acanthochromis polyacanthus* at hatching. Symbols show estimated marginal means (±95% confidence intervals) of (a) standard length, (b) weight (mg), (c) condition, and (d) yolk area (mm^2). Means are adjusted for the random effects of female ID nested within sump. Condition is back-transformed to show the estimated weight (in mg) for the average standard length of 5.20 mm. Sample sizes (i.e. number of F_2 juveniles) are given next to symbols, with raw values shown as jittered points

plasticity (Munday et al. 2008, Nilsson et al. 2009, Gardiner et al. 2010). While it is possible that fish may sustain their growth in nature by increasing their food intake or conversion efficacy (Elliott & Elliott 2010, Volkoff & Rønnestad 2020), it is likely that growth potential may be further reduced by climate-induced patchiness or limitation in planktonic food availability (Hays et al. 2005, Cavole et al. 2016, Barbeaux et al. 2020).

Warming during development left long-lasting impacts on reproductive performance. Adults that developed in the warm temperature were shorter in SL and produced ~60% fewer eggs across the breeding season. This supports a widely observed pattern whereby larger fish produce more and/or larger eggs (reviewed in Barneche et al. 2018) and could have substantial implications for population replenishment considering the extremely high mortality during early life stages of marine fish (Almany & Webster 2006). Previous studies have also highlighted such developmental effects whereby fish that are developmentally (Spinks et al. 2021) or transgenerationally (Donelson et al. 2016) exposed to elevated temperature produce fewer eggs even when returned to optimal conditions. Since post-maturation temperature did not influence the number of eggs produced, reduced fecundity may not simply be due to additional metabolic costs incurred from elevated temperature (Nilsson et al. 2009, Gardiner et al. 2010, Rummer et al. 2014). Instead, developmental impacts, such as those on gonadal development (Pankhurst & King 2010, Wang et al. 2010, Butzge et al. 2021) or the proper establishment of the reproductive–endocrine axis (Lema et al. 2024), may have left long-lasting impacts on the reproductive physiology of adults.

Elevated temperature during reproduction impacted egg quality, as adults reproducing in the post-maturation warm temperature produced significantly smaller eggs (~11.4%). As adults in the post-maturation warm treatment were lighter for a given length (~4.2%) and maternal condition positively correlated with egg size, smaller eggs produced by fish in the post-maturation warm treatment may have been due to reduced energy allocation for reproduction at elevated temperature (Van Der Kraak & Pankhurst 1997, Donelson et al. 2010, Pankhurst & King 2010). Alternatively, as clutch sizes were similar across post-maturation treatments (~255 eggs), our results may also represent an energetic trade-off whereby fecundity at elevated temperature was maintained at the expense of egg size and provisioning (Fleming & Gross 1990, Brown & Shine 2009). Interestingly, the reduction in egg size with post-maturation warming did not lead to measurable impacts on offspring quality and no offspring traits were impacted by parental thermal treatment both during development and/or after maturation. This lack of treatment effect was evident even in juvenile traits that were positively correlated with egg size. Specifically, juveniles from the post-maturation warm treatment were only slightly shorter (~0.13 mm) and had slightly smaller yolk reserve (~0.10 mm^2) than those from the post-maturation control. In both instances, patterns were better explained by egg size rather than parental thermal treatment (Table S9). More broadly, limited differences in offspring traits across treatments may also result from variations in yolk utilization (Fukuhara 1990, Rombough 1997) and linear growth (Wen et al. 2013, Rioual et al. 2021) during embryogenesis, which could buffer the effects of parental thermal experience. As size (Fisher et al. 2000, Marshall et al. 2006) and physical condition (Hoey & McCormick 2004, Grorud-Colvert & Sponaugle 2006) can be important determinants for juvenile survival, we expect the survival of newly hatched juveniles to be similar across the parental treatments.

The spiny chromis damselfish *A. polyacanthus* has been extensively studied with respect to thermal sensitivity and plasticity. Previous studies have almost exclusively simulated warming using seasonal temperature cycles alone. The present study is among the first (but see Spinks et al. 2021) to include diurnal variation (±0.6°C) alongside seasonal fluctuations and highlights that diurnal variation could potentially magnify the impacts of developing in elevated temperatures. For example, previous studies without diurnal variation reported complete restoration of reproductive capacity (back to control levels) when 1.5°C warming is experienced throughout development (Donelson et al. 2014, 2016). In contrast, in the present study and Spinks et al. (2021), which both include diurnal variation, negative impacts on reproduction remain. Compared to constant temperatures, fluctuating temperatures could have different impacts on physiological performance (Peng et al. 2014, Morash et al. 2018, Rodgers et al. 2018, Salinas et al. 2019, Guzzo et al. 2019, Li et al. 2021) or lead to different phenotypic pathways when experienced during development (Schaefer & Ryan 2006, Duc & Massey 2023). As such, the addition of diurnal fluctuations (±0.6°C) may have accentuated physiological sensitivity by making conditions even more stressful (the magnitude of warming is 2.1°C rather than 1.5°C) or by altering the capacity of plasticity through more heterogenous environments (Burgess & Marshall 2014, Herman et al. 2014, Leimar & McNamara 2015). Since the present study did not have a treatment that only included seasonal fluctuations, other factors (e.g. collection location of fish, different genetics) could also have caused the observed differences between studies. It is also possible that reproductive impacts documented in this study are accentuated due to the relatively low sample size (Ioannidis 2008, Ioannidis et al. 2011, Button et al. 2013). However, the broad findings of reproductive thermal sensitivity generally match with previous work on this species and other marine fish (e.g. Soria et al. 2008, Donelson et al. 2010, Pankhurst & Munday 2011, Vikingstad et al. 2016). Thus, the present findings underscore the importance of incorporating natural temperature fluctuations in experiments to accurately understand biological responses to climate change (Reed et al. 2010, Vasseur et al. 2014, Burton et al. 2020).

Additionally, whether reproductive performance in elevated temperatures is influenced by extended warming can be explored by comparing reproductive performance in the first (Spinks et al. 2021) and second (present study) breeding seasons. Comparing total eggs produced per pair, reproductive output in elevated temperature improved after an additional year of warming. In the first breeding season, control—warm pairs produced 21% fewer eggs than control—control pairs (Spinks et al. 2021), whereas in the second breeding season, they produced similar numbers of eggs (1% fewer). Similarly, while no pairs from the warm—warm treatment reproduced in the first breeding season (Spinks et al. 2021), warm—warm pairs produced an equivalent of 62% of eggs compared to control—control pairs in the second season. These findings contrast with past studies showing limited capacity of reef fish to acclimate to warming through reversible plasticity (Munday et al. 2008, Donelson et al. 2010, Nilsson et al. 2010, Donelson & Munday 2012, Bowden et al. 2014, Miller et al. 2015, Rodgers et al. 2019) and suggests that adult fish may have some capacity to maintain their performance in elevated temperatures given sufficient time. However, it is also important to note that impacts of developing in elevated temperatures remained regardless of a further year at present-day temperature, as warm—control pairs continued to produce 40% fewer eggs than control—control pairs in the second breeding season. We are cautious in drawing emphatic conclusions from these results because the total number of breeding pairs participating in the study is relatively low (3—6 per treatment), and different breeding individuals between Spinks et al. (2021) and the present study may have also caused the disparity. Nevertheless, these findings could highlight the importance of long-term experiments to accurately assess warming impacts across an individual's lifetime.

Our work strongly supports the fact that the timing of thermal experience is important for understanding organismal responses to climate change. Warming during development proved especially influential, leading to smaller adults that produced significantly fewer eggs even in their second breeding season. Our work also underscores the importance of including variation around the average when experimentally simulating thermal environments, as the addition of a ±0.6°C diurnal cycle on top of the seasonal 1.5°C treatment led to accentuated impacts. Finally, some negative impacts on reproduction were mitigated with a longer duration of warming after maturation, indicating that reproductive performance in warm temperatures may improve across an individual's lifetime. These findings point to the increasing importance of research quantifying how the timing, duration, and variability of environmental experience influence phenotypic responses, allowing us to better understand thermal performance in an increasingly warmer and less predictable ocean.

Data accessibility. All data used in this study and copies of the statistical analysis are available from https://doi.org/10.25903/0bbh-bv95.

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