Phenotypic plasticity to warming in coral reef fishes: the importance of sex and exposure timing within and between generations

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October, 2021

For the degree of Doctor of Philosophy in Natural and Physical Sciences

ARC Centre of Excellence for Coral Reef Studies

James Cook University

Acknowledgements

I must first thank my supervisors, Philip Munday and Jennifer Donelson, for their unrelenting support. This PhD has been extremely challenging for me due to a number of health issues, yet Phil and Jenni have been patient and encouraging throughout. Phil is one of the few great, but still humble scientists. His gentle guidance kept me on the path to success. He showed me how to be a rigorous and ethical scientist and better writer and speaker. Jenni's hands-on help during experiments was a life-saver! I also greatly appreciate the time she took to discuss results. She's always a step ahead of everyone with her amazing ideas! Jenni showed me how to be a strong but caring leader.

I would also like to thank my close collaborator Lucrezia Bonzi. Her help towards the end of the multigenerational experiment was invaluable. Another collaborator, Tim Ravasi, has also provided tremendous encouragement throughout my PhD. Thanks also to the Ravasi lab members for great scientific discussions. Importantly, my experiments would not have been possible without the staff at the Marine and Aquaculture Research Facility Unit at James Cook University. I especially want to thank Simon Wever who was the technician for my experiments and really made an effort to have the facility running seamlessly. I am also deeply indebted to my many volunteers and the Munday lab, especially Shannon McMahon, for their help with my experiments and good-humour during the difficult times.

I would like to thank Alana Grech for her mentorship, Janet Swanson for her admin assistance and our lovely chats, and countless other ARC CoE for Coral Reef Studies colleagues for their support. A big thank you to Murray Logan for introducing me to Bayesian statistics and expanding my knowledge in the R programming language.

I am greatly indebted to Taka Shimada, friends and family for the strong foundation they provided, allowing me to overcome my personal challenges. Without their support I could not have completed this PhD. I must also thank my pet budgie for always making me laugh. Towards the end of thesis writing, one of my medical conditions flared and I used speech-to-text software to finish. Funnily enough the software interpreted my budgie's shrills as swear words. I apologise if any were left behind! Last of all, I must acknowledge the Spiny chromis damselfish, what a wonderful species to work with! I especially enjoyed their courting dances and parental behaviours.

I feel very privileged to have been on this journey and value everyone who has been a part of it. Thanks for helping me get here.

Statement of the Contribution of Others

This thesis includes collaborative work with my supervisors Dr. Jennifer Donelson and Prof. Philip Munday, along with Lucrezia Bonzi and Prof. Timothy Ravasi. While undertaking these collaborations, I was responsible for the project design, data collection, analysis, interpretation of results, and writing. My co-authors provided intellectual guidance, editorial assistance, technical help and financial support.

Research funding was provided by the ARC Centre of Excellence for Coral Reef Studies (P. Munday and R. Spinks), King Abdullah University of Science and Technology (P. Munday, T. Ravasi, J. Donelson), and Sea World Research and Rescue Foundation Inc (R. Spinks, P.Munday, J. Donelson). Stipends were provided by James Cook University, King Abdullah University of Science and Technology, and the ARC Centre of Excellence for Coral Reef Studies. James Cook University provided laboratory space and funding for technicians at the Marine and Aquaculture Research Facilities Unit.

General Abstract

Rising temperatures owing to anthropogenic climate change are affecting the physiological performance and behaviour of individual animals, with flow-on effects to populations, communities and ecosystems. Tropical ectotherms, in particular, are expected to suffer from higher temperatures since they may already be living close to their upper thermal limits. However, the effects of predicted future warming on animal populations also depends on their ability to cope via phenotypic plasticity and genetic adaptation. Phenotypic plasticity is predicted to be especially important in responding to rapid climate change because it can operate over a much faster timescale than genetic adaptation. Phenotypic plasticity is the ability of a genotype to produce different phenotypes in response to environmental variation. Phenotypic flexibility during early life (developmental plasticity) has been recognised for some time and there is increasing evidence that environmental conditions in one generation can influence the phenotype of future generations (parental effects); however, major knowledge gaps remain. Little is known about how the sex of the individual and the duration and ontogenetic timing of exposure to environmental change may influence current and future generations' performance. Furthermore, plasticity is not always beneficial and may potentially exacerbate the negative effects of climate change. Understanding these gaps will improve predictions of the effects of climate change on tropical ectotherms and the capacity for phenotypic plasticity to maintain or improve performance as warming continues. This thesis uses an experimental approach to test whether the duration and ontogenetic stage of exposure to elevated temperature, and sex of the individual, influence within- and between-generation phenotypic plasticity in a coral reef damselfish, *Acanthochromis polyacanthus*.

Whether phenotypic plasticity occurs, or not, may depend on the ontogenetic timing and duration of exposure to different environmental conditions. On coral reefs, heatwave conditions often coincide with periods of peak recruitment of juvenile fishes. Marine heatwaves currently last for days, but are projected to last much longer under future climate change scenarios. In **Chapter 2** I tested whether differences in the duration of high temperature exposure (+2°C) from hatching influence predator evasion, body size, and upper thermal limits of *A. polyacanthus* later in development. While upper thermal limits of juveniles were not affected, exposure to +2°C for one- and three-months improved escape performance. Yet the three-month exposed juveniles were smaller in size. These results show that exposure to higher temperature early in life can induce beneficial developmental plasticity, but this may trade-off with other important fitness-related traits.

The developmental environment can have lasting effects on individual performance, yet if this differs by sex, or how it may influence future generations, is poorly understood. Due to the thermally sensitive nature of reproductive physiology, warming can disrupt reproduction or lead to fewer and poorer quality progeny. Therefore, in **Chapter 3** I exposed mothers and fathers during their development, reproduction, or both life stages, to present-day or elevated temperature (+1.5°C; 8 treatments) and measured reproductive performance and hatchling quality. As expected, mothers and fathers that developed in present-day temperature, but reproduced in +1.5°C, produced fewer and poorer quality offspring. Yet mothers that developed in +1.5°C, but reproduced in present-day temperature, produced more and higher quality offspring. By contrast there was a reduction in reproductive output when fathers developed in +1.5°C, but reproduced in present-day temperature. Finally, females that were exposed to +1.5°C in both developmental and reproductive stages did not breed. This indicates that female fish developing during a marine heatwave, but reproducing in present-day conditions, may have superior reproductive performance than males developing in heatwaves, or females developing in usual thermal conditions. However, the lack of reproduction from a permanent increase in temperature throughout life suggests a limit to plasticity, with consequences to population sustainability. These results demonstrate that the duration and ontogenetic timing of exposure to warming, and which sex is exposed, influence fecundity and offspring quality.

Parental effects induced by elevated temperature can modify the performance of offspring, yet it is unknown if mothers and fathers contribute differently based their timing of exposure to high temperature and how this interacts with the offspring environment. In some fishes, higher temperature can decrease average body size and skew sex ratios. Thus, in **Chapter 4** I investigated maternal and paternal effects and exposure timing of warming on offspring size, body condition, and sex ratios. Of the six parental treatments that bred in **Chapter 3**, I reared their offspring in present-day and future temperatures (+0.75°C and +1.5°C). I found that offspring reared in warmer temperatures from control parents were shorter but in higher condition, which indicates beneficial developmental plasticity. However, when mothers, fathers, or both parents were exposed to warming, whether it be during development and/or reproduction, their offspring were lighter and in lower condition, regardless of the offspring's rearing temperature. Poorer condition is likely detrimental to offspring success. By contrast, no significant effects of warming on offspring sex ratios were observed. These results suggest that parental effects exacerbate within generation effects of elevated temperature on body size, and have direct effects on the condition of juvenile *A. polyacanthus*, with potential fitness implications. Although some other trends were observed between the parental treatments, the

results broadly show that when, how long and which parent is exposed to warming did not substantially influence the traits measured in this chapter.

In **Chapter 5** I explored how maternal and paternal effects of warming during development interact with offspring environments to affect offspring swimming performance. Using a subset of offspring reared in all three temperatures from **Chapter 4** I swam the juveniles in present-day, +0.75°C and +1.5°C temperatures and measured maximum swimming speed. As expected, juvenile fish swam faster in warmer water. There was also evidence for beneficial developmental plasticity, with offspring reared in +0.75°C from present-day exposed parents swimming faster. Strikingly, mothers or fathers independently exposed to warming during development produced faster swimming offspring compared to offspring where both parents developed in present-day or elevated temperatures. Faster swimming in offspring of thermally mismatched parents was most pronounced when they developed in present-day temperature. It may be that faster swimming is a side-effect of the mismatch in thermal conditions between parents and across generations. A higher maximal swimming speed may be beneficial, however, it could also come with greater energetic costs and trade-off with other traits. This could explain why offspring with both mothers and fathers reared in warmer temperature did not increase their swimming speed, as it was already optimal for the overall energy budget. This study highlights the importance of considering maternal, paternal, and biparental contributions as parent-specific results would have been masked if only the combined effects from mothers and fathers were considered.

This thesis demonstrates that within- and between-generation phenotypic plasticity can help tropical ectotherms cope with climate change in some circumstances, but there may be costs or trade-offs with other traits. In other cases, phenotypic plasticity appears to be maladaptive and may worsen the effects of warming, which could accelerate population decline. My results establish that early life experiences, that last at least a month, in both males and females, can have lasting effects on individual performance in a coral reef fish, and importantly, interact with the next generations' performance. Overall, my research findings highlight the complexity of predicting the effects of ocean warming on tropical fish populations, since the duration, ontogenetic timing, and sex-linked experiences to warming interact, within and between generations. Further careful experimentation, in a wider variety of species, will be critical to accurately predict responses of marine fishes to climate change and their capacity to adjust through phenotypic plasticity.

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Chapter 1 General Introduction

Phenotypic plasticity is the ability of a genotype to produce distinct phenotypes in response to different environments (Pigliucci, 2001; Stearns, 1989a; West-Eberhard, 2003). Once considered a nuisance in evolutionary studies, phenotypic plasticity now plays a fundamental role in our understanding of how organisms develop and interact with their current environment (Pigliucci, 2005). Environmentally-induced plastic responses may range from morphological modifications to alterations in physiology, life history, and behaviour. An organism that responds rapidly to its surrounding environment is more likely to succeed and in many cases plasticity improves performance and therefore is considered adaptive (e.g. Charmantier et al., 2008; Dantzer et al., 2013; Knop & Reusser, 2012). However, the machinery for phenotypic flexibility may be costly or trade-off with other important fitness related traits (DeWitt, Sih, & Wilson, 1998; Murren et al., 2015). It's also possible for phenotypic plasticity to be maladaptive when the environment is incorrectly anticipated and thus the phenotype is poorly matched (Auld, Agrawal, & Relyea, 2010). Nevertheless, phenotypic plasticity is an integral part of generating the phenotypic diversity observed in nature and may enable organisms to adjust rapidly to environmental change.

How an individual's (or genotype's) phenotype varies across environments can be represented graphically as a reaction norm (Woltereck, 1909). A flat reaction norm or horizontal line indicates no change in that individual's phenotype across environmental variation (figure 1.1A), whereas a slope of the reaction norm indicates phenotypic plasticity (figure 1.1B). When the reaction norms of two individuals (or genotypes) are plotted and the slopes vary, this is called a genotype by environment (G×E) interaction (figure 1.1C; Ghalambor, McKay, Carroll, & Reznick, 2007). That is, variation in the slopes of the reaction norms exist based on genetics, or in other words some genotypes are more plastic than others (i.e. genotype 1 in figure 1.1C is more plastic than genotype 2). At a population-level, how the mean phenotype of multiple genotypes varies across environmental variation can also be observed, for example in figure 1.1C the mean phenotype has a positive slope since both genotypes' reaction norms increase from left to right (Pigliucci, 2005). It's important to acknowledge, however, that this example is an overly simplistic view of genotypes, the environment, and phenotypes (Burggren, 2020). Since genetic variation for plasticity within populations exists, and assuming the slopes of the reaction norms are positively correlated with fitness, phenotypic plasticity can evolve by responding to natural selection (Schlichting & Pigliucci, 1998). Alternatively, plasticity may facilitate evolution through the accommodation of a favorable phenotype during development that exploits a new

environment and natural selection may then genetically assimilate that novel phenotype (i.e. phenotypic accommodation and genetic assimilation; Pigliucci, Murren, & Schlichting, 2006; Schmalhausen, 1949; Waddington, 1953; West-Eberhard, 2003). While plasticity can lead or follow evolution, with rapid climate change it is expected the initial phenotypic response to environmental change will lead because it can occur within an individual's generation, thereby potentially increasing that individual's performance and fitness which selection can act on.

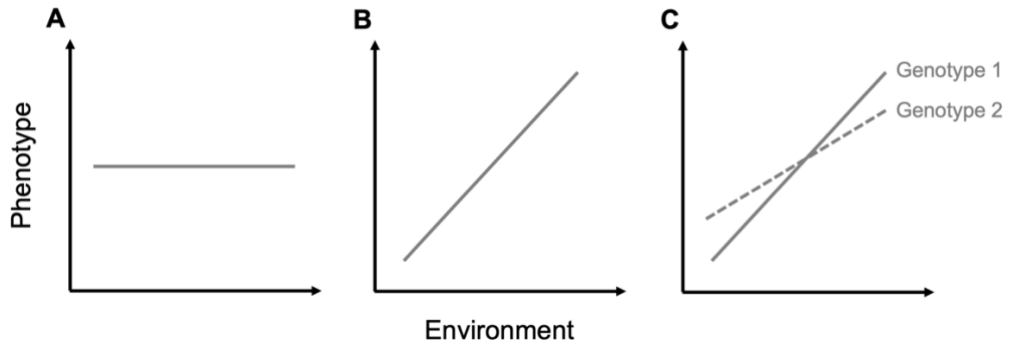

Figure 1.1 Reaction norms. In each panel the vertical axis is the phenotype and horizontal axis the environment. In A) no change has occurred in that genotype's (or individual's) phenotype across environmental variation, whereas in B) change has occurred and this indicates phenotypic plasticity. Finally, C) illustrates a genotype by environment (G×E) interaction where different genotypes (or individuals) exhibit different levels of phenotypic plasticity.

Phenotypic plasticity can occur both within and between generations. When the environment of past generations influences the phenotype of the current generation it has been termed in the literature as parental effects, intergenerational effects/plasticity, multigenerational effects/plasticity, or transgenerational effects/plasticity (Bell & Hellmann, 2019; Bonduriansky & Day, 2009; Donelan et al., 2020; Donelson, Salinas, Munday, & Shama, 2018; Uller, Nakagawa, & English, 2013; Yin, Zhou, Lin, Li, & Zhang, 2019). In biomedical and epigenetic fields, the term transgenerational is often used when environmental exposure of great-grandparents or grandparents results in phenotypic change in the offspring (i.e. the first generation where primordial germ cells, embryos, and foetuses are unexposed), while intergenerational is used when parental exposure results in phenotypic change in the offspring (Heard & Martienssen, 2014; Nilsson, Sadler-Riggleman, & Skinner, 2018). In ecology the term transgenerational is used more loosely and can mean phenotypic change in the offspring owing to environmental exposure of the parents (and then is equivalent to parental effects or

intergenerational effects/plasticity) or further generations back (Bell & Hellmann, 2019; Donelan et al., 2020; Munday, 2014; Tariel, Plénet, & Luquet, 2020; Yin et al., 2019). Sometimes the term transgenerational is reserved for circumstances where past and current generations' experience interact (Burgess & Marshall, 2014; Donelson et al., 2018; Marshall & Uller, 2007; Salinas, Brown, Mangel, & Munch, 2013; Uller et al., 2013). In this thesis I use the term parental effects and make note of specific types when it helps to differentiate them. Occasionally, within-generation plasticity and parental effects are further divided into whether cues provide information about future environments (coined informational) or are a result of change (coined somatic state-based) because these may evolve under different conditions (Nettle & Bateson, 2015). While this can provide further insight, I refrain from explicitly stating these differences in my thesis to reduce complexity.

Theory predicts that within-generation plasticity and parental effects will be favoured in different circumstances of environmental variation, but are not mutually exclusive (Burgess & Marshall, 2014; Donelson et al., 2018). In the case of within-generation plasticity, it would be expected to occur when the environment varies within a single generation (Herman, Spencer, Donohue, & Sultan, 2014). While parental effects typically occur when the environment varies between generations but parents can effectively predict the offspring environment (Burgess & Marshall, 2014; Herman et al., 2014; Lind et al., 2020). There are also circumstances where parents do not need to predict the offspring environment for environment-induced parental effects to evolve (Bonduriansky & Crean, 2018), which I will expand on later.

Within-generation plasticity and parental effects are often said to have a non-genetic basis. In this thesis, I use the term 'non-genetic' to describe processes that do not involve modification of the DNA sequence, even though the DNA sequence is fundamental to these processes (West-Eberhard, 2003). By contrast, evolution is a genetic mechanism that enables adaptation by natural selection and may take many generations. Thus, phenotypic plasticity may operate over faster timescales than adaptation by natural selection, potentially allowing organisms to adjust rapidly to changing environments (Geoghegan & Spencer, 2012; Klironomos, Berg, & Collins, 2013). The underlying non-genetic processes of plasticity may involve epigenetics (e.g. DNA methylation, histone modification, and small non-coding RNAs), cell structures (e.g. mitochondria), hormones, nutrients (e.g. milk allocation), or behaviours (e.g. learning; Bonduriansky & Day, 2009; Ho & Burggren, 2010). While there is still some debate as to whether adaptive plasticity is widespread in nature, and there is generally limited

direct evidence for it, rapid environmental change produces circumstances where plasticity may play a role in adaptation, even if historically it has not.

1.1 Within-generation plasticity

The type of plasticity expressed within a generation may depend on the ontogenetic timing of exposure. Environmental conditions experienced during early development can induce strong and often permanent phenotypic change known as developmental plasticity (West-Eberhard, 2003). Critical windows, or sensitive periods, are an essential part of developmental plasticity. A certain environmental exposure during a critical window in development can shift the phenotype from the normally expected developmental trajectory (Burggren, 2020). By contrast, adult phenotypic adjustments are usually reversible (i.e. reversible plasticity) and are expected to be comparatively less sensitive (Angilletta Jr, 2009). Collectively, developmental plasticity and reversible plasticity can be referred to as within-generation plasticity (Donelson et al., 2018). A fascinating example of developmental versus reversible plasticity in humans follows. Visual deprivation owing to cataracts during the first year of a child's life can result in permanent visual deficits (Wiesel, 1982). Reversal of the visual deprivation outside of this critical window shows the eyes are unharmed but still poor vision persists likely due to a reorganisation of the brain (i.e. neuroplasticity; Hensch, 2005; Hensch & Bilimoria, 2012). By contrast, adults affected by cataracts, once removed have normal vision (Wiesel, 1982). Therefore, to predict whether phenotypic plasticity will transpire in a single generation, it is important to know when and how long the critical window in development occurs and to consider the ontogenetic timing of environmental exposure. Furthermore, it's important to understand whether the timing of environmental exposure in one generation could affect future generations (Burton & Metcalfe, 2014).

1.2 Parental effects

The parental environment may influence the offspring phenotype via the transfer of non-genetic information, which in this thesis I define as parental effects. For example, wild red squirrel mothers exposed to actual or perceived high-density environments produced faster growing offspring (Dantzer et al., 2013). Faster growth in high-density environments would likely increase the chance that offspring survive their first winter. This parental effect, or more specifically maternal effect, appeared to be due to increased maternal hormones (glucocorticoids). This example highlights how non-genetic effects provide the opportunity for

parents to alter their offspring phenotype depending on the environmental conditions experienced during their lifetime.

Parental effects may occur alone, additively to within-generation plasticity, or interact with the offspring environment. If we consider the offspring reaction norm when parents are exposed to different environments (figure 1), we observe carry-over parental effects when the parental environment influences offspring phenotype either alone (figure 1.2A) or additively to within-generation plasticity in offspring (figure 1.2B; Bonduriansky & Crean, 2018; Donelson et al., 2018; Jablonka et al., 1995; Salinas, Brown, Mangel, & Munch, 2013). Bonduriansky and Crean (2018) argue that carry-over (or as they say condition-transfer) parental effects are often adaptive because the transfer of high parental condition to offspring will tend to enhance offspring performance, and thus ultimately results in increased fitness of parents. Jablonka et al. (1995) also illustrated through modelling that carry-over parental effects are most advantageous in randomly varying environments. However, Marshall and Uller (2007) suggest that under stressful environmental conditions they are mostly non-adaptive. For instance, high temperature exposure to zebrafish during a critical window can skew sex ratios and this male bias is passed to the next generation (Valdivieso, Ribas, Monleón-Getino, Orbán, & Piferrer, 2020). Bonduriansky and Crean (2018) argue that the transfer of a poor parental phenotype to offspring can still result in positive net selection, because poor condition parents generally produce fewer offspring than high condition parents and any trait that enhances the fitness of high condition individuals will tend to be beneficial on average. Nevertheless, researchers agree carry-over parental effects are likely widespread (Bonduriansky & Crean, 2018; Jablonka et al., 1995).

In contrast to carry-over parental effects, anticipatory parental effects (sometimes referred to as transgenerational effects/plasticity) are typically observed when the parental environment has an interactive effect on offspring phenotype (figure 1.2C) such that parents predict offspring conditions in order to produce progeny with the best phenotype for that environment (Donelson et al., 2018; Marshall & Uller, 2007). Anticipatory parental effects are contingent on environmental predictability and, therefore, are most likely to occur when the parental environment is a good predictor of the offspring environment. This means anticipatory parental effects may be maladaptive when offspring conditions differ from those experienced by parents (Burgess & Marshall, 2014). The risk of a mismatch between the predicted and actual environment will tend to select against anticipatory parental effects and may explain the weak

evidence across taxa (Bonduriansky & Crean, 2018; Radersma, Hegg, Noble, & Uller, 2018; Sánchez-Tójar et al., 2020; Uller et al., 2013).

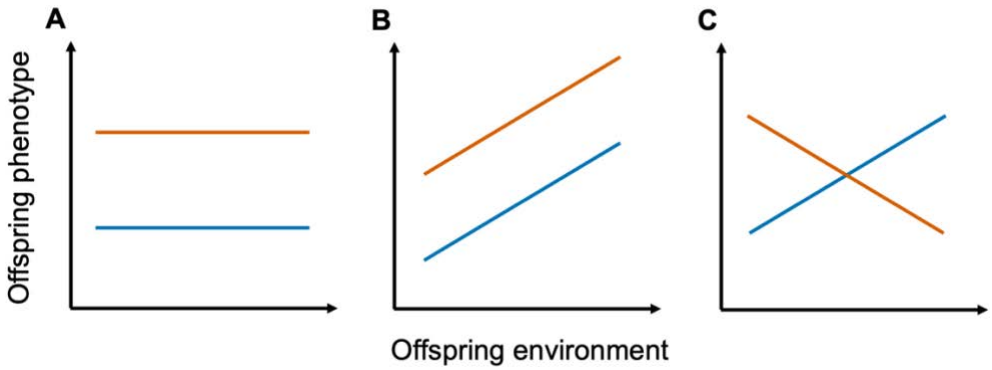

Figure 1.2 Reaction norms under different parental effects. In each panel the vertical axis is offspring phenotype and the horizontal axis the environment in which offspring were raised. The blue and orange lines represent different parental environments. In A) only the parental environment has an effect on offspring phenotype, i.e. carry-over parental effects. In B) there is an additive effect of parent and offspring environments on offspring phenotype but no interaction, i.e. within-generation plasticity in offspring plus carry-over parental effects. In C) there is an interaction and the parental environment modifies both the intercept and slope of the offspring reaction norm, i.e. anticipatory parental effects.

A question that arises about parental effects is whether mothers and fathers have equal or different contributions to their occurrence and magnitude of effect. Maternal effects have long been recognised as a significant source of non-genetic phenotypic variation in a variety of taxa, arising from differences in embryonic nutritional provisioning (Mousseau & Fox, 1998). For example, mothers can match the phenotype of their offspring to changes in the local environment, as seed beetles do by laying larger eggs on thick-coated seeds to provide extra resources for offspring to successfully bore through (Fox, Thakar, & Mousseau, 1997). Furthermore, mitochondria are typically maternally inherited and, being the powerhouse of life, they can have important implications on offspring phenotypes (Ghiselli & Milani, 2020). Paternal effects, however, are often assumed to be absent or much less important than maternal effects, especially in organisms that lack conventional paternal provisioning and care (Crean & Bonduriansky, 2014). But the contribution of fathers to their offspring's phenotype is not

restricted to genes alone, and non-genetic contributions via the paternal line seems increasingly likely (Crean, Dwyer, & Marshall, 2013; Yin et al., 2019). For instance, prepubescent smoking in men may contribute to obesity in sons, possibly through inheritance of altered epigenetic marks (Nilsson, Sadler-Riggleman, & Skinner, 2018; Northstone, Golding, Smith, Miller, & Pembrey, 2014; Pembrey et al., 2006).

Sex-specific parental effects are most likely to evolve when males and females have different reproductive strategies, predation pressures, parasitism, or socialising and foraging behaviours (Burke, Nakagawa, & Bonduriansky, 2020; Lewis et al., 2002; Magnhagen, 1991; Ruckstuhl, 2007; Zuk & McKean, 1996). Sex-specific patterns may also be found in offspring, whereby the mother's environment influences only daughters or the father's environment influences only sons or any combination of these depending on whether the mother's or father's environment is a better predictor of the offspring environment (Hellmann, Bukhari, Deno, & Bell, 2020). Even when the sexes are alike, it is possible that mothers and fathers experience different environments when temporal environmental variation exists or large spatial areas are traversed leading to the potential for differing maternal and paternal effects. Owing to the logistical challenges of multigenerational experiments, how the environmental experiences of mothers, fathers or both parents affect daughters and sons is not well understood. However, recently some well-designed experiments using stickleback fish (*Gasterosteus aculeatus*) have begun to shed light on this. Lehto and Tinghitella (2020) exposed mothers, fathers, or both parents to predators and measured their daughters' mating behaviour in comparison to daughters of unexposed parents. Maternal and paternal predator exposure independently resulted in daughters who preferred less conspicuous males, but when both parents were predator exposed a reverse in these mate preferences were observed. Unexpectedly, the combined effects of maternal and paternal predator exposure were not cumulative. Non-additive effects of predator exposed mothers and fathers on offspring survival and gene expression were also discovered by Hellmann et al. (2020). Further, Hellmann et al. (2020) found paternal predator exposure resulted in sons that were risk-prone, whereas maternal predator exposure resulted in more anxious sons and daughters. These studies highlight the importance of disentangling the relative non-genetic roles of mothers and fathers on offspring phenotype to accurately predict the magnitude and direction of parental effects.

Whether maternal or paternal effects occur may also depend on the ontogenetic timing or length of parental exposure to environmental change (Donelson, Wong, Booth, & Munday, 2016; Fuxjäger et al., 2019; Salinas & Munch, 2012; Shama et al., 2016; Suckling et al., 2015). For

example, developmental exposure to stressful conditions, such as a heatwave, can allow individuals to cope better with those same conditions later in life and this benefit may be passed to offspring (Donelson, Munday, McCormick, & Pitcher, 2012). By contrast, parents that reproduce during stressful conditions may have insufficient resources for their offspring, resulting in negative parental effects (Donelson et al., 2016; Fuxjäger et al., 2019; Radersma et al., 2018). Alternatively, certain life stages of the mother's or father's experience may be better predictors of offspring environment due to life-history. Lastly, brief exposure to environmental change may induce a parental effect but there is increased chance of a mismatch with the offspring environment (Salinas & Munch, 2012). Therefore, to predict the occurrence and outcome of parental effects, we must understand how the ontogenetic timing and duration of maternal and paternal exposure affects the offspring phenotype.

1.3 Impact of global warming on individuals and ecosystems

Industralisation has led to increased anthropogenic greenhouse gas emissions and consequently is causing the Earth's temperature to rise. Human activities have already caused nearly 1°C of global warming above pre-industrial levels (IPCC, 2018). Projections based on current emissions (RCP8.5 scenario) estimate a 2.6-4.8°C average increase in global air temperature by 2100 compared to the recent past (1985-2005; IPCC, 2019). Rising temperatures can have profound effects on the morphology, physiology, and behaviour of individual animals. For instance, elevated temperature has been shown to reduce body size, halt reproduction, and induce risky behaviours (Nagelkerken & Munday, 2016; Sheridan & Bickford, 2011; Wong & Candolin, 2015; Zeh et al., 2012). By reducing individual fitness, this can scale to issues with population sustainability and eventually alter ecosystem functioning and services. For example, corals bleach (i.e. expel their algal symbionts) during heat stress and when bleaching is prolonged many corals can die (Hughes et al., 2003, 2018). Coral reefs are vital habitat for an enormous diversity of organisms, and the loss of living coral and its associated physical structure can cause a decline in diversity and abundance of many reef-associated species (Cheal, Wilson, Emslie, Dolman, & Sweatman, 2008; G. P. Jones, McCormick, Srinivasan, & Eagle, 2004). Humans also rely on living coral reefs for food, tourism, recreation, and coastal protection therefore, their loss can impair economic and social well-being. Widespread marine heatwaves, as seen in recent years, can induce mass coral mortality resulting in a subsequent change in community structure or if recovery is not possible a regime shift to algae-dominant reefs (Eakin, Sweatman, & Brainard, 2019; Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015; Hughes et al., 2018).

For ectotherms, global warming can be energetically costly since their metabolic rate scales directly with environmental temperature (Dillon, Wang, & Huey, 2010; Gillooly, Brown, West, Savage, & Charnov, 2001). Furthermore, greater vulnerability to warming is observed in tropical ectotherms, especially in the marine realm, likely reflecting their higher intrinsic sensitivity (Comte & Olden, 2017; Pinsky, Eikeset, McCauley, Payne, & Sunday, 2019; Sunday, Bates, & Dulvy, 2011; Tewksbury, Huey, & Deutsch, 2008). By this I mean tropical ectotherms appear to live close to their upper thermal limits, and therefore, may have narrower thermal safety margins than their temperate counterparts (Deutsch et al., 2008; Pinsky et al., 2019; Tewksbury et al., 2008). This is due to their low past rates of evolution in upper thermal limits likely owing to the relatively stable thermal environment in the tropics (Comte & Olden, 2017). While a narrow thermal performance range can reduce maintenance costs (Farrell & Pörtner, 2008), beyond this thermal range there will be steep declines in performance and overall fitness (Hoffmann, Sørensen, & Loeschcke, 2003). Projections show that even when the increase in environmental temperature seems small, the resulting changes in body size and metabolic rate of tropical ectotherms is large (Cheung et al., 2013; Dillon et al., 2010).

1.4 How ectotherms use phenotypic plasticity to cope with warming

Distributional shifts away from warmer areas is a common population-level response but results in local extinctions, potential consequences to individual fitness, or is not feasible for some organisms (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Pecl et al., 2017). Phenotypic plasticity and adaptation by natural selection may allow phenotypic adjustment to warmer conditions, possibly preventing local population declines or extinction. Phenotypic plasticity is predicted to be especially important in responding to climate change because it can operate over a much faster timescale than adaptation (Geoghegan & Spencer, 2012; Kleronomos et al., 2013). There is considerable evidence for within-generation plasticity, particularly developmental plasticity, in response to warming in ectotherms (Byrne, 2011; Gunderson & Stillman, 2015; Reusch, 2014; Riddell, Odom, Damm, & Sears, 2018; Sandoval-Castillo et al., 2020; Seebacher, White, & Franklin, 2015). For example, a comprehensive study found zebrafish exposed to high temperature during their embryonic period (critical window), swam faster when experiencing that same temperature as an adult (Scott & Johnston, 2012). These brief high temperature experiences may be relevant to heatwaves, which are increasing in frequency, duration, and intensity owing to climate change (Frölicher, Fischer, & Gruber, 2018; Perkins-Kirkpatrick & Gibson, 2017). Interestingly, embryonic exposure to elevated temperature also allowed the

zebrafish to maintain swimming performance in cooler waters (Scott & Johnston, 2012). These changes were explained by muscle fiber type composition and differently expressed genes. However, within-generation plastic responses to warming are not always beneficial or may have limitations (Kim, Metcalfe, da Silva, & Velando, 2017; Rodgers, Donelson, McCormick, & Munday, 2018; Zeh et al., 2012). Moreover, few studies consider the duration of exposure to elevated temperature and how this may influence the phenotype within a single generation and whether it extends beyond that current generation. Therefore, a greater understanding of within-generation plasticity to higher temperature is needed, in addition to how it may interact with subsequent generations, to predict it's use for ectotherms to cope with global warming.

Evidence of parental effects in response to warming in ectotherms is gradually increasing (Chakravarti et al., 2016; Donelson et al., 2018; Roth & Landis, 2017; Salinas & Munch, 2012; Schwanz, 2016), but there is a lack of studies on tropical species, which are expected to be the most vulnerable to warming (Comte & Olden, 2017; Pinsky et al., 2019). Moreover, how the ontogenetic timing and duration of maternal and paternal exposure affects the offspring phenotype is not well understood in a global warming context (Donelan et al., 2020; Donelson et al., 2018). A rare exception in a temperate marine fish (*Gasterosteus aculeatus*) has explored maternal and paternal effects to ocean warming across two life-stages (development and reproduction; Fuxjäger et al., 2019; Shama et al., 2016; Shama, Strobel, Mark, & Wegner, 2014; Shama & Wegner, 2014). Mothers that developed at elevated temperature provided benefits to offspring by increasing mitochondrial respiratory capacity and thus efficiency and body size (Shama et al., 2016, 2014). However, if females developed in present-day temperature but reproduced in elevated temperature, they produced smaller eggs, reiterating the importance of the timing of exposure (Fuxjäger et al., 2019). Furthermore, fathers exposed to warming had a positive effect on early offspring size, but negative effect on their sons mating success (Fuxjäger et al., 2019; Shama & Wegner, 2014). In addition, interactions were present between life-stages and generations (Fuxjäger et al., 2019). This example illustrates the complexity of predicting the possible effects of warming on phenotypic plasticity across multiple generations. Similar studies in other species, especially tropical ectotherms that are thought to be most at risk from rising temperature, are needed to understand if and how parental effects may help offspring cope with warming.

1.5 Study species

My thesis examines the potential for within-generation plasticity and parental effects to predicted global warming on coral reef fishes. I used an experimental approach, breeding and rearing the coral reef damselfish, *Acanthochromis polyacanthus* (spiny chromis Bleeker 1855; figure 1.3), over two generations in future ocean warming scenarios. *A. polyacanthus* is an ideal species for this approach because it is widespread in the Indo-Australian archipelago (Robertson, 1973), easy to breed and rear in captivity, and has been extensively used to test the effects of higher temperature on individual performance and fitness (Bowden et al., 2014; Clark, Roche, Binning, Speers-Roesch, & Sundin, 2017; Donelson, Munday, McCormick, Pankhurst, & Pankhurst, 2010; Munday, Kingsford, O'Callaghan, & Donelson, 2008; Nilsson, Crawley, Lunde, & Munday, 2009; Rodgers et al., 2018; Rodgers, Donelson, & Munday, 2017; Zarco-Perelló, Pratchett, & Liao, 2012).

Male and female *A. polyacanthus* are morphologically identical, although can be distinguished by the shape of their genital papillae (Hilder & Pankhurst, 2003; Robertson, 1973). Sexual maturation is attained within approximately two years (Donelson, McCormick, Booth, & Munday, 2014) where they will form monogamous pairs and breed primarily during the summer months (Robertson, 1973; Thresher, 1985). They lay clutches of 100-550 eggs that are relatively large in size (~4 mm length), adhered to the substrate within caves on the reef (figure 1.3; Kavanagh, 2000; Robertson, 1973; Thresher, 1985). Both parents provide care during embryonic development and in the initial weeks to months post hatching (Kavanagh, 2000; figure 1.3). For this reason, they typically produce only one to two clutches in a season (Thresher, 1985). Unlike other coral reef fishes, *A. polyacanthus* lack of a dispersal larval stage. Instead, they develop directly, which means they can be captive reared with high success. In the wild, it also implies that offspring will likely take up residence near to where they hatched. Adult *A. polyacanthus* are reasonably site attached and typically have small home ranges (Miller-Sims, Gerlach, Kingsford, & Atema, 2008), which may signify they are unlikely to migrate to more favourable conditions under climate warming. *A. polyacanthus* live predominantly in shallow waters (0-15 m) and have been found at a maximum depth of 65 m (Jankowski, Graham, & Jones, 2015; Lieske & Myers, 1994). However, it's unlikely they move to deeper waters for relief as the thermocline on corals reefs in the Great Barrier Reef often sits much deeper than their maximum depth (Walther, Kingsford, & McCulloch, 2013). This means only <0.1°C difference in temperature from 10 to 60 m appears to exist in the cooler months and ≤1°C difference in the warmer months, although during the 2016 summer marine heatwave temperatures at 10 and 60 m were almost

equal (Frade et al., 2018). Consequently, the capacity for a plastic physiological or morphological response to environmental change is likely to be essential for future persistence.

A. polyacanthus juveniles or adults exposed short-term to 1.5-3°C above current-day average summer temperatures have exhibited higher resting metabolic rates and lower aerobic capacity, larger gill surface areas, reduced growth, decreased breeding, and declines in sperm production (Bowden et al., 2014; Donelson et al., 2010; Munday et al., 2008). In fact, low-latitude populations of adult *A. polyacanthus* struggled to survive when acutely exposed to a 1.5-3°C increase in local present-day average temperatures (Rodgers et al., 2018; Rummer et al., 2014). Generally, this suggests beneficial adjustments to elevated temperatures via reversible plasticity are limited. Similar responses have been found in other coral reef fishes (Bowden et al., 2014; Nilsson et al., 2009; Rummer et al., 2014). By contrast, developmental exposure of *A. polyacanthus* to +3°C from hatching allowed partial compensation of resting metabolic rate and an improvement in escape performance (Donelson, Munday, McCormick, & Nilsson, 2011; Jarrold & Munday, 2018). However, sex ratios were skewed and trade-offs with body size and condition occurred (Donelson et al., 2011; Jarrold & Munday, 2018; Rodgers et al., 2017). While we know that exposure to warming during early life is important in *A. polyacanthus* to induce developmental plasticity (whether it be a positive or negative response), we do not know the exact length of exposure required (Donelson & Munday, 2015; Munday et al., 2008; Rodgers et al., 2017). This is especially relevant to marine heatwaves that often coincide with periods of peak recruitment of juvenile fishes.

Beneficial parental effects under future warm ocean temperatures were also present in *A. polyacanthus*. Anticipatory parental effects are expected since *A. polyacanthus* are site attached and lack a dispersal larval stage, which suggests the parental environment is a good predictor of the offspring environment. For instance, restoration of offspring aerobic capacity and sex ratios occurred in warmer temperatures providing parents had been reared in +1.5 or +3°C (Donelson & Munday, 2015; Donelson, Munday, McCormick, et al., 2012). Yet restoration of the sex ratios in offspring was not observed if parents were exposed to warming only during reproduction (Donelson & Munday, 2015), indicating that the developmental environment of parents may be the best predictor of offspring developmental conditions (Burton & Metcalfe, 2014) or that parents are unable to adjust offspring sex without that developmental experience. How the ontogenetic timing of parental exposure to warming affects other important fitness-related traits in offspring is unknown. Furthermore, we do not know the relative non-genetic

roles of *A. polyacanthus* mothers and fathers on offspring phenotype and how this interacts with the timing of parental exposure.

Figure 1.3 Study species. The top photograph is an Acanthochromis polyacanthus adult with offspring on the Agincourt reefs of the Great Barrier Reef, Australia. Credit: eschlogl / iNaturalist.org. License: CC by Attribution-NonCommercial. The below photograph is an A. polyacanthus egg clutch adhered to a terracotta pot, the day prior to hatching. Credit: Rachel Spinks.

1.5 Thesis aims and outline

This thesis examines the potential for *A. polyacanthus* to adjust to projected global warming through phenotypic plasticity within and between generations. Furthermore, it considers the timing and duration of exposure to higher temperatures (i.e. during marine heatwave events) on current and future generations and the relative non-genetic roles of mothers and fathers on offspring fitness. While the effects of warming on many organisms are well documented and to

a lesser extent their ability to use within-generation plasticity and parental effects to better cope, how time and sex impact plasticity and thus the ability of organisms to persist in the future has remained largely unexplored. To investigate this, I used an experimental, whole organism approach.

In **Chapter 2,** I tested whether differences in the duration of high temperature exposure (+2°C) from hatching influence predator evasion, body size, and upper thermal limits of *A. polyacanthus* later in development. The results of this chapter shed light on the length of exposure required to induce beneficial developmental plasticity and show that, depending on the duration, trade-offs with other important fitness-related traits may arise.

In **Chapter 3,** I exposed females and males during their development, reproduction, or both life stages, to present-day or elevated temperature (+1.5°C; 8 different treatments in total) and measured reproductive performance and the quality of these pairs newly hatched offspring. The results of this chapter demonstrate how ontogenetic exposure timing, duration, and sex can influence fecundity and offspring performance in both positive and negative ways.

In **Chapter 4,** I investigated the timing of maternal and paternal exposure to elevated temperature on offspring size, body condition, and sex ratios. Of the six parental treatments that bred in **Chapter 3**, I reared their offspring in present-day and future temperatures (+0.75°C and +1.5°C). The results of this chapter suggest that any parental experience to warming may be detrimental to offspring performance, although small differences due to parental ontogenetic exposure timing, duration, and sex still exist.

In **Chapter 5,** I explored how maternal and paternal developmental exposure to warming affects offspring swimming performance. Using a subset of offspring reared in all three temperatures from **Chapter 4** I swam the juveniles in present-day, +0.75°C and +1.5°C temperatures and measured maximum swimming speed. This study highlights the importance of considering maternal, paternal, and biparental contributions as parent-specific results would have been masked if only the combined effects from mothers and fathers were considered.

Together these four chapters advance our knowledge on phenotypic plasticity, including how the ontogenetic timing, duration, and sex can influence phenotypic outcomes within and between generations. My findings also improve our understanding of how coral reef fishes may adjust to global warming. While developmental plasticity appeared mostly beneficial, particularly for females and their offspring, I also observed costs of plasticity, trade-offs among traits, and unexpected maladaptive responses. Phenotypic plasticity within and between

generations will likely be important for organisms to persist on a future, warm planet, however, it will probably be dependent on when the exposure to warming occurred, for how long, and which sex experienced it.

Chapter 2 Developmental Effects of Heatwave Conditions on the Early Life Stages of a Coral Reef Fish

This chapter was published in The Journal of Experimental Biology (2019) 222, jeb202713, DOI:10.1242/jeb.202713. Authors: Rachel K. Spinks, Philip L. Munday, and Jennifer M. Donelson.

The associated data are available on Research Data JCU repository, DOI:10.25903/5d01d448c3756, and the R script of analyses is available in the publication's supplementary material.

2.1 Abstract

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

2.2 Introduction

Marine heatwaves are damaging marine ecosystems worldwide, from mass bleaching of coral reefs (Hughes et al., 2017) to kelp forest die off (Wernberg et al., 2016). Defined as periods of abnormally high sea surface temperatures that persist for days to months, marine heatwaves have increased in frequency, duration, and intensity over the past century and can be linked to global warming (Frölicher et al., 2018; Oliver et al., 2018). Elevated sea temperature can have adverse impacts on marine life by increasing metabolic demands (Deutsch et al., 2015), affecting growth and survival (Pepin, 1991; Sheridan and Bickford, 2011) and modifying behaviour (Nagelkerken and Munday, 2016). Furthermore, environmental extremes can have a greater impact on individuals and populations than gradual changes in average conditions (Vasseur et al., 2014). Importantly, marine heatwave conditions frequently coincide with periods of high juvenile abundance, and may therefore have fundamental effects on development and recruitment to the adult population.

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

development can affect marine species, lasting effects will ultimately depend on the timing and duration of exposure to higher temperature and the traits involved.

As fishes are ectotherms with limited capacity for internal temperature regulation, environmental temperature directly influences the rate of cellular processes and physiological performance (Jobling, 1997). Consequently, higher water temperature will increase metabolic rate, influencing key biological processes that regulate life-history traits (Schulte, 2015). Tropical fishes can be affected by relatively small increases in temperature, with changes to aerobic scope (Nilsson et al., 2009), activity patterns (Johansen et al., 2014), escape responses (Allan et al., 2015), developmental rates (Green and Fisher, 2004), and growth (Munday et al., 2008). This suggests they are currently living close to their thermal optima during summer and only have a safety margin of a few degrees Celsius before negative effects occur (Rummer et al., 2014; McLeod et al., 2014). The most thermally sensitive time for fishes is during reproduction and early development (Pankhurst & Munday, 2011; Pörtner & Peck, 2010). As coral reef fishes reproduce during spring and summer, it increases the probability that heatwave conditions will coincide with early developmental stages. This provides the opportunity for exposure during early life to produce lasting phenotypic changes to later life stages. Recent experiments have shown that continuous exposure to elevated water temperature throughout development can alter performance (Donelson, 2015). For example, exposure to 1.5-3°C above summer averages during early life can partially restore or even enhance aerobic scope of damselfish (Donelson et al., 2011; Donelson, 2015; Grenchik et al., 2013). By contrast, predominately negative developmental effects on body size, aerobic scope, escape performance, and swimming ability were observed in juvenile wrasses exposed to 2°C above summer average (Motson & Donelson, 2017). These results suggest that exposure to higher temperature from early life may induce developmental changes to morphology or behaviour that in turn influence individual performance; however, all the studies conducted to date have employed designs focused on testing the effect of long-term increases in average water temperature associated with global warming. Whether exposure to higher temperature for a restricted duration during early life, such as with heatwave conditions, induces lasting phenotypic change is currently unknown.

Here, I exposed juvenile spiny chromis damselfish, *Acanthochromis polyacanthus*, to elevated temperature (2°C above summer average) for increasing lengths of time to test if there were lasting effects on their individual performance. Specifically, I exposed damselfish to 3, 7, 30, or 108 days of elevated temperature from hatching to determine the influence on the resulting phenotypes compared to fish reared at present-day control temperature (for 108 days).

The Great Barrier Reef recently experienced water temperatures of 1-2°C above current average summer temperatures, for days to weeks at a time (figure 2.1; Hughes et al., 2017). If global warming is constrained to a 1.5°C average increase above preindustrial levels, marine heatwaves are expected to last on average 39 days and be up to 1.1°C hotter than in preindustrial times (Frölicher et al., 2018). However, if carbon emissions are not curtailed, a business-as-usual scenario projects marine heatwaves will likely last on average 112 days and be up to 2.5°C hotter than in preindustrial times (Frölicher et al., 2018). I therefore chose timeframes and a temperature treatment that would sit between recent local observations and future global predictions. After the 108 days' post-hatching (dph) rearing period, I measured a range of traits relevant to individual performance, including escape response (fast-starts), body size, and critical thermal maximum, to determine if increasing lengths of exposure to elevated temperature influenced the development and performance of these traits. Escape responses are predation avoidance techniques that entail high accelerations and a change in direction, aimed at displacing the prey away from the threat (Eaton, 1984). To establish if developmental plasticity influenced the kinematics of an escape response, fish from all exposure duration treatments were tested at both control and elevated temperatures. Testing fish at both temperatures was completed so that effects due to developmental conditions (i.e. plasticity) could be disentangled from the effect of the final temperature each treatment ended at on 108 days (Schulte et al., 2011). I also measured body size, which is a key fitness related trait in juvenile fishes that links to competitive ability and predation risk (Goatley & Bellwood, 2016; Poulos & McCormick, 2015; Sogard, 1997). Reduced growth rates and smaller body size with increased warming is a commonly observed trend in fishes (Cheung et al., 2013; Munday et al., 2008). Lastly, I measured critical thermal maximum (CT_{max}) as it defines the upper lethal limits at which an animal's locomotor activity becomes disorganised and can no longer escape from conditions that will lead to death (Cowles & Bogert, 1944). While some studies show that CT_{max} of adult reef fishes can increase following exposure to elevated temperatures (Barker, Horodysky, & Kerstetter, 2018; Eme & Bennett, 2009; Habary, Johansen, Nay, Steffensen, & Rummer, 2016) other studies have found little change in CT_{max} (Donelson, 2015). Whether experiences to elevated temperature for a restricted duration during early life has a persistent effect on CT_{max} is unknown.

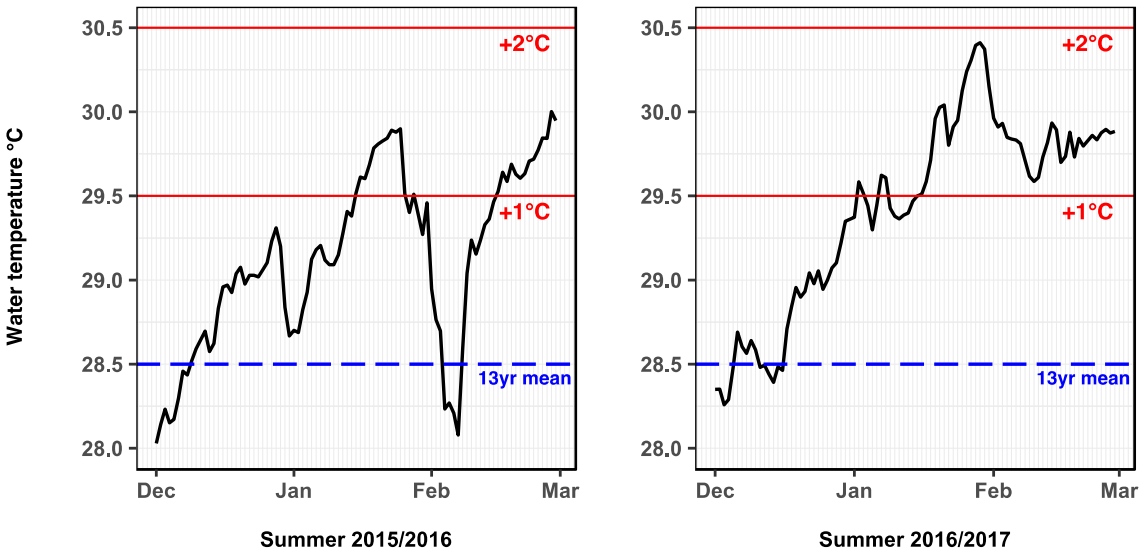

Figure 2.1 Daily mean sea temperatures during marine heatwaves. Recorded during the 2015/2016 and 2016/2017 Austral summers at 6 m depth on Orpheus Island reef, central Great Barrier Reef (AIMS, 2017). The blue dashed lines show the summer average from 2002-2015 (AIMS, 2016).

2.3 Methods

2.3.1 Study Species

A. polyacanthus (Bleeker 1855) is a widespread Indo-Australian coral reef damselfish that forms monogamous pairs (Miller-Sims et al., 2008; Robertson, 1973) and breeds during the warmer months (most often between October to February; Robertson, 1973). They lay clutches of 100-500 eggs, adhered to substrate, with an average embryonic period of 9 days at 28.5°C (Chapter 3; Kavanagh, 2000). This species lacks a pelagic larval stage (Robertson, 1973) and juveniles remain with their parents for a few months after hatching (Kavanagh, 2000; Robertson, 1973).

2.3.2 Broodstock

Adult *A. polyacanthus* were collected from Bramble Reef (18° 22′ S, 146° 40′ E) on the central Great Barrier Reef and Holmes Reef (16° 28′ S, 147° 52′ E) in the Coral Sea in July 2015 and 2016, respectively. Fish were transported to the Marine and Aquaculture Research Facility at James Cook University, Townsville Australia, and housed in breeding pairs within 42 L tanks, each with half a terracotta pot as shelter and spawning site. Tanks were supplied with a continuous flow of seawater from a 25,000 L recirculating system with precise temperature control (6 x 2 kW Control Distributions custom-built heaters, Carlton, NSW, Australia; 18 kW Solarwise

chiller EXC341RC, Kingston, QLD, Australia; PR Electronics temperature transmitter 5333A ±0.1°C, Rønde, Denmark). Water quality was maintained with mechanical, biological, and ultra violet filtration, as well as protein skimming. Pairs were kept at seasonally cycling, present-day sea temperature for the region where fish were collected based on temperature loggers around Orpheus Island from 2002-2015 at 0.2-14.6m depth (appendix figure 2.1; AIMS, 2016). Light levels followed the natural seasonal cycle. Adult fish were fed *ad libitum* on commercial fish pellets (INVE Aquaculture NRD G12, Salt Lake City, UT, USA) at least once a day. When summer average water temperature (28.5°C) was reached in November 2016, aquaria were checked every morning for the presence of newly laid egg clutches. The first clutches from four pairs laid in December 2016 and January 2017 were used in this experiment. All clutches remained with parents during embryonic development allowing them to provide nest care as occurs in the wild. Within 3 hours of hatching, the offspring were removed from the parents' tank and transferred to experimental treatments.

2.3.3 Experimental Design

Juveniles were reared for 108 dph at the average summer sea temperature for the central Great Barrier Reef (present-day control mean: 28.5°C) and in four treatments where they were exposed to a higher temperature (+2°C mean: 30.5°C) for 3, 7, or 30 dph, or for the entire 108 days of the experiment. After exposure to the elevated temperature for 3, 7, or 30 dph, juveniles were returned to the control temperature until performance testing. For each of the four clutches, newly hatched juveniles were randomly allocated to three replicate tanks at each treatment level (i.e. 15 tanks total per clutch), with 10 fish per tank. To represent natural reef conditions, a diurnal temperature cycle (±0.6°C) that rose at day and cooled at night, was employed for the present-day control and elevated temperatures. Newly hatched juveniles were transferred to experimental tanks in a 2 L tub that was then half-submerged in the tank with partial water exchange over 3 hours to slowly equilibrate temperature. This protocol was also employed for the temperature shifts at 3, 7, and 30 dph. To prevent handling bias, the fish reared for 108 dph at the present-day control and the elevated treatment were likewise shifted to new aquaria at 30 dph. No mortalities occurred during these transitions. In total, only 0.5% mortality occurred during the 108-day rearing period. Illumination was kept at the average summer photoperiod (12:12 hrs) throughout the experiment. Feeding rates were the same for all treatments. Juveniles were fed approximately 10 mg (dried cyst weight) per individual of live *Artemia nauplii* the first three days, then weaned to 2 mg per individual of 200-400 µm size

NRD pellets and finally increased to 3 mg per individual of 500-800 µm size NRD pellets at 30 dph (INVE Aquaculture, Salt Lake City, UT, USA). This is considered a high feeding level (at an average of 1-2% of their body weight) for captive *A. polyacanthus* on an energy-rich formulated diet (Donelson et al., 2010). Prior to trials, fish were starved for 12 hours. This research was conducted under James Cook University's ethics approval A2315.

2.3.4 Escape Response

To determine the influence of thermal exposure duration on escape performance, I measured six escape response traits at the end of the experiment (between 109–121dph) in fish that had been exposed to an average of +2°C for 0, 3, 7, 30, and 108 dph. For each treatment level, I measured the escape responses at the mean present-day control (28.5°C) and mean elevated temperature (30.5°C). Fish were randomly allocated to these performance temperatures a minimum of seven days prior to trials to prevent an acute stress reaction. All fish were shifted, following the same temperature transition protocol described above, even if they stayed in the same temperature. Trials were conducted between 0900–1800, over seven days. To prevent any time or day bias, testing of fish was random across treatments and tank replicates. Using a standard protocol by Allan et al. (2014), fish were introduced into a circular arena (∅ 32 cm, H 9 cm) via a water filled container and allowed two minutes to acclimate. The arena sat inside an opaque plastic tank (∅ 64 cm, 348 L) with a transparent acrylic bottom to allow responses to be filmed from below via a high-speed camera (480 fps, Casio Exilim EX-ZR2000, Tokyo, Japan) pointed at a mirror on a 45° angle. A 5 cm line drawn on the bottom of the tank enabled calibration for video analysis. The top and underside of the tank were covered to prevent disturbance to the fish. Illumination of the arena was via LED strips (Arlec cool white 1000 lumens, Blackburn North, VIC, Australia) wrapped around the outside of the tank. The arena was filled to 4 cm to minimise vertical movement of the fish in the water column. A 25 W glass heater (Kong's Aqua one 11301, Ingelburn, NSW, Australia) with a digital thermostat (Full Gauge Controls Tic-17RGTi, Canoas, Brazil) that maintained the set-point temperature within ±0.1°C, was immersed between the arena and tank wall, along with four air stones for oxygenation.

Fish were startled once only by the release of a conical shaped, black-tipped magnet from an electromagnetic device. The magnet was secured to the electromagnet device via fishing line so that the tapered tip just touched the water surface. To prevent a premature response associated with visual stimulation, the magnet fell through a PVC pipe (∅ 4 cm) suspended 1 cm above the water surface. Fish were startled at least one body length away from

the arena's wall to reduce edge effects on escape responses (Eaton & Emberley, 1991). When the stimulus first hit the water surface, I measured the direction the fish were facing in reference to the stimulus and the distance between the fish and the stimulus to determine if there were any differences between treatments and performance temperatures. After 10 minutes, if the fish did not leave the arena's wall, no startle attempt was made and the trial ended. After each trial, the arena was flushed with new water, and after five trials the whole tank was drained and refilled.

The following escape response traits were measured:

Response latency – defined as the time (milliseconds) between the onset of the stimulus hitting the water's surface and the first detectable movement of the head.

Response probability – classified as a C-start escape response or non-Cstart response in reaction to the stimulus. A C-start escape response begins at the first detectable movement of the head, the fish makes a C-shape rotation and ends when the body straightens out (akin to stages 1 and 2 defined by Domenici and Blake (1997)).

Escape maximum speed – defined as the maximum speed (m s^{-1}) reached at any point during a C-start escape response.

Escape mean speed – defined as the average speed (m s^{-1}) during a C-start escape response within a given time interval of 20 ms (this corresponds to the average C-start escape response for all fish).

Escape distance – defined as the total distance (mm) covered during a C-start escape response within a given time interval of 20 ms.

Escape direction – defined as the direction (°) after the C-start escape rotation, relative to the stimulus.

Larger fish are known to perform faster escape responses and travel further, therefore fish standard length was included as a covariate in escape speed and distance models (Domenici & Blake, 1997). Additionally, initial orientation of the fish from the stimulus is known to influence escape direction hence orientation on stimulus impact was included as a covariate in the escape direction model (Domenici & Blake, 1993). Videos were analysed blind using ImageJ

software v. 1.50i (Schneider et al., 2012) with the manual tracking plugin. I standardised tracking from the head of the fish (~10% of the standard length) as it was the most reliable area to track.

2.3.5 Body Size

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

2.3.6 Critical Thermal Maximum

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

2.3.7 Statistical Analyses

I chose to analyse the data in a Bayesian framework because it grants exploration of complex random-effects structure, handles unbalanced designs with ease, has more appropriate estimates of uncertainty, and it allows integration of prior information (Kruschke, 2015). All analyses were performed in R v. 3.5.1 (R Core Team, 2020) with figures created in the ggplot2 package (Wickham, 2016).

Hierarchical Mixed Models. I used the rstanarm package v. 2.17.4 (Goodrich, Gabry, Ali, & Brilleman, 2020) to implement Bayesian hierarchical mixed models. All models included the fixed effect of exposure duration treatment (0, 3, 7, 30, 108 dph at +2°C). Escape response models also included the fixed effect of performance temperature (28.5°C, 30.5°C) and when appropriate, the covariates standard length and escape duration (table 2.1). Body size models included sex as a covariate and the CT_{max} model included standard length (table 2.1). Continuous covariates were centred to improve model optimisation and scaled for comparison purposes. All relevant interactions were explored. The random effects structure was defined by fish tank nested within family for all models, with CT_{max} models additionally including trial date (table 2.1). This structure was necessary to control for non-independence of fish raised in the same tank, fish from the same family, fish in the same CT_{max} trial, and to account for the hierarchical experimental design (Harrison et al., 2018). A random-intercept model was used in all circumstances except for standard length, weight, and CT_{max} (table 2.1). In these latter three, a random-intercept and random-slope model fitted best (visually and via model selection) because the slopes differed between the dependent variable (e.g. weight) and the treatments.

Table 2.1 Final models fitted.

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

Note. A cross (x) indicates an interaction. Orientation on stimulus impact was transformed to cosine and sine components to maintain the circular characteristics when used as a covariate. NA, not applicable.

Bayesian models incorporate prior knowledge, which can be: 1) informative if specific knowledge exists, 2) weakly informative if general knowledge exists, or 3) non-informative if no knowledge exists. I specified an informative normal intercept prior mean for standard length, weight, and CT_{max} (appendix table 2.1). The informative priors were selected because Rodgers et al. (2017) found that *A. polyacanthus* exposed to present-day sea temperatures for 90 dph were an average standard length of 33.99 mm and wet weight of 1.21 g. Additionally, the critical thermal maxima of two lower latitude populations of *A. polyacanthus* were defined at an average of 37.07°C (Rodgers et al., 2018) and 36.58°C (Clark et al., 2017). In all other instances I specified weakly informative intercept, slope, and error standard deviation priors (appendix table 2.1). A half Cauchy distribution was selected for the error standard deviation priors as it is ideal for weakly informative priors and hierarchical models (Gelman, 2006). Visual posterior checks confirmed that priors never heavily influenced the posteriors. Models used Hamiltonian Monte Carlo, which is a Markov Chain Monte Carlo (MCMC) method, and were run with three chains using the No-U-Turn Sampler (NUTS) for 5000 iterations, with the first 1000 samples discarded. Every second sample was thinned. Thus, posterior distributions derived from each chain comprised a minimum of 2000 samples.

Model Validation and Selection. Models were confirmed to be well mixed and converge on a stable posterior via visual inspection of the trace plots. In some models, better mixing of chains was encouraged by reducing the step size and thus controlling the resolution of the sampler. Densities of all three chains closely agreed and were normally distributed. $\hat{R}$ values were below 1.05 and effective samples were a minimum of 2000. Posterior distributions closely reflected the actual distribution of the data. When relevant, the residuals plotted against the fitted values were randomly dispersed around zero and the Quantile-Quantile plots illustrated normality. I compared models for predictive accuracy using Pareto smoothed importance sampling leave-one-out cross-validation (PSIS-LOO), implemented by the loo package v. 2.0.0 (Vehtari, Gelman, & Gabry, 2017). This is performed by estimating the difference in the models' expected log predicted density (elpd) and generating a LOO information criterion, LOOIC, along with its' standard error. LOOIC is similar to Akaike information criterion (Akaike, 1973), but takes priors into account and makes no distributional assumption about the posterior (Vehtari et al., 2017). Models with lower LOOIC values are expected to have higher predictive accuracy. Final models were selected for inference based on LOOIC values and parsimony (Bates et al., 2015). General conclusions were identical for models with similar LOOIC values.

Circular Models. Escape direction and orientation on stimulus impact are periodic dependent variables requiring circular analysis methods. I used the bpnreg package v. 1.0.0 (Cremers, 2018) to implement a Bayesian embedding approach to circular regression with a projected Gaussian distribution. Both models included exposure duration treatment and performance temperature as fixed effects, while the escape direction model also included orientation on stimulus impact as a covariate, which was transformed to sine and cosine components to maintain its circular characteristics (appendix table 2.1; Pewsey, Neuhäuser, & Ruxton, 2013). I was unable to run mixed effects models due to the unbalanced design of the random effects with no known alternative software. Directional variables were converted to radian prior to analysis and then transformed to circular coefficients as per Cremers et al. (2018) and Cremers and Klugkist (2018). The default weakly informative priors were used, which specified a normal intercept prior of 0 for each of the two components and a prior precision matrix with diagonal values equal to 0.001 (Cremers, 2018; Cremers et al., 2018). Models used the same MCMC method, NUTS sampler, iterations, and warm up as above except only one chain could be run. Model validation was also as previously mentioned, however model selection was via the Bayesian Watanabe-Akaike information criterion (WAIC; Watanabe, 2010).

Estimates of Uncertainty and Significance. Bayesian estimates of uncertainty, such as the highest posterior density credible intervals used in this study, include the true value of the response. Contrast this with 95% confidence intervals used in a Frequentist framework with which the response *may* fall 95 out of 100 times within this interval. In this study, strong evidence for an effect (i.e. statistical significance) is defined when a 95% credible interval (CI) does not intersect with zero. Moderate evidence for an effect is inferred when 85% of a CI lies to one side of zero.

2.4 Results

2.4.1 Escape Response

Response latency demonstrated no evidence (i.e. the ≥85% CI intersected with zero) of a difference between the exposure duration treatments or between performance temperatures (figure 2.2A). All but one fish, which was facing 180° away from the stimulus upon impact, responded to the stimulus. The majority (~80%) of reactions were C-start escape responses. Non-Cstart responses included moving slowing backwards or even towards the stimulus in a few instances. However, there was no evidence of a difference in the probability of producing a non-Cstart response between the exposure duration treatments and control (figure 2.2B).

Performance temperature also did not influence the probability of producing a non-Cstart response (figure 2.2B).

Exposure to +2°C for 30 and 108 dph resulted in moderate evidence towards an increase in escape mean speed (i.e. the 85% CI did not intersect with zero – *30 dph* 0.026 m s^{-1} to 0.189 m s^{-1}; *108 dph* 0.016 m s^{-1} to 0.183 m s^{-1}), with fish escaping on average 9% (30 dph) and 8% (108 dph) faster than control fish (figure 2.2C). Performance temperature did not influence the escape mean speed of juveniles (figure 2.2C). There was strong evidence (i.e. the 95% CI did not intersect with zero) that longer fish escaped faster, irrespective of thermal exposure duration (appendix figure 2.2A). The fixed effects of the escape mean speed model (treatment, performance temperature, standard length, and C-start duration) explained 12% variability (marginal r^2), whilst the whole model including the random effects (tank nested in family) explained 14% variability (conditional r^2) of escape mean speed. Escape maximum speed, on the other hand, showed no evidence of a difference between the exposure duration treatments and 30.5°C performance temperature compared to control (figure 2.2D). Escape maximum speed also showed no influence by fish standard length (appendix figure 2.2B).

Fish exposed for 30 dph and 108 dph to elevated temperatures showed moderate evidence of travelling further during an escape response (85% CI *30 dph* 0.518 mm to 4.18 mm; *108 dph* 0.012 mm to 3.89 mm), with fish travelling on average 10% (30 dph) and 8% (108 dph) further than control fish (figure 2.2E). There was strong evidence that longer fish moved further, irrespective of thermal exposure duration (appendix figure 2.2C). The model explained 61% (marginal r^2) and 62% (conditional r^2) variability of escape distance. Fish exposed for 108 dph to elevated temperatures showed strong evidence of a change in escape direction, which was on average 34° clockwise from control fish, albeit all fish escaped in a direction away from the stimulus (figure 2.2F; appendix table 2.2). There was no evidence that performance temperature had an effect on escape direction (figure 2.2F; appendix table 2.2).

The orientation fish were facing on stimulus impact demonstrated no evidence of a difference in exposure duration treatments compared to control (appendix figure 2.3A). There was strong evidence for a ~20° clockwise change in orientation on stimulus impact in fish performing an escape at 30.5°C compared with 28.5°C (control), but the orientation was still towards the stimulus (appendix figure 2.3A). Escape direction model fits were greatly improved when adding orientation on stimulus impact as a covariate. Finally, fish exposed for 30 dph showed strong evidence of being closer to the stimulus on impact compared to control fish (mean diff. -9.14 mm, 95% CI -16.8 mm to -1.97 mm; appendix figure 2.3B), yet treatment and

performance temperature explained only 4% variability (marginal r^2) of this distance. Escape response model fits were not improved when adding distance from stimulus as a covariate.

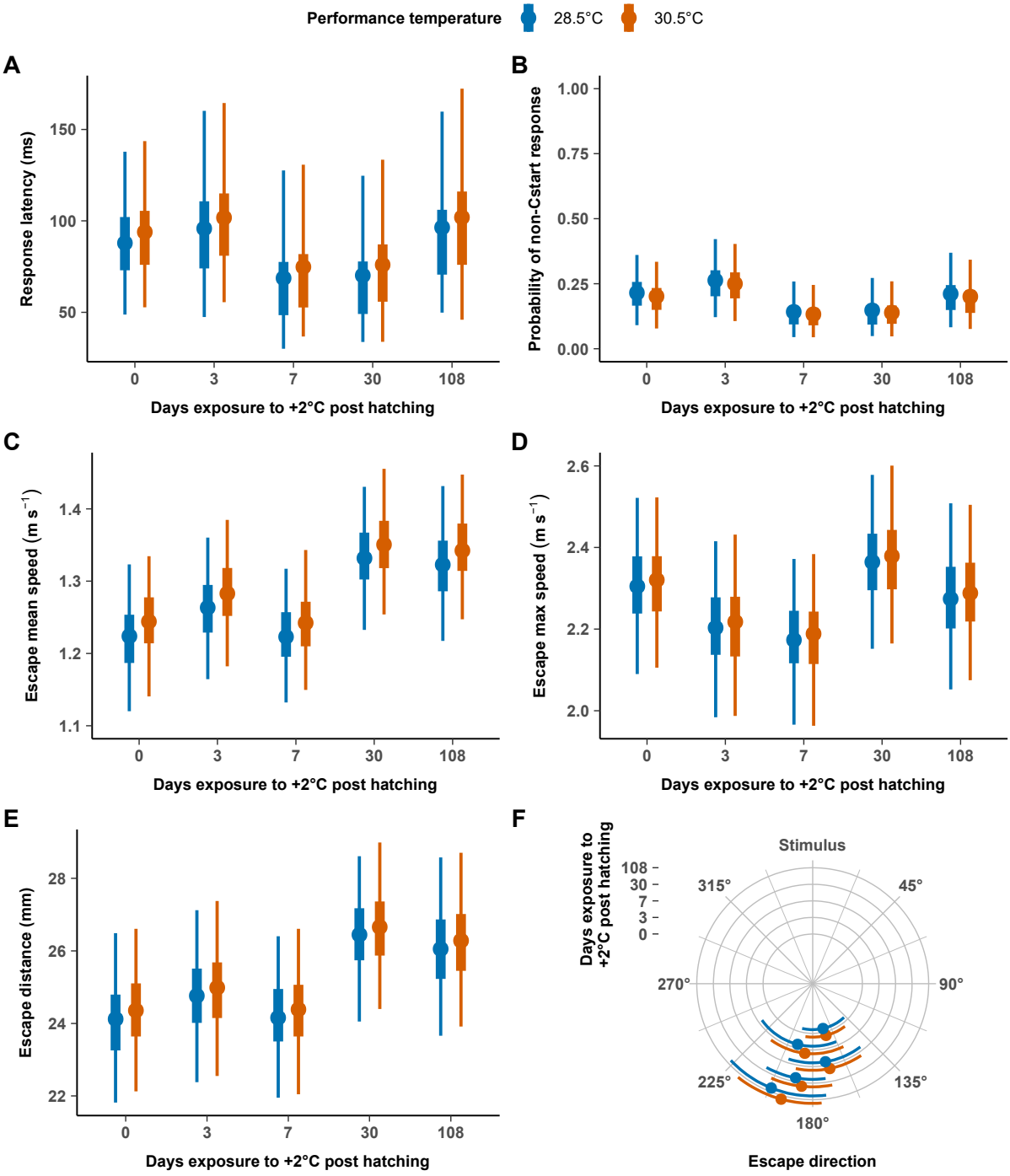

Figure 2.2 Escape performance. Bayesian posterior medians (circles), 50% credible intervals (thick lines), and 95% credible intervals (thin lines) of fish ***A*** *response latency,* ***B*** *probability of non-Cstart response,* ***C*** *escape mean speed,* ***D*** *escape maximum speed, and* ***E*** *escape distance. Plots C-E are held at the average standard length (36.10 mm) of fish tested.* ***F*** *escape direction shows Bayesian posterior means (circles) and 95% credible intervals (lines). Numbers on the left correspond (from top to bottom) to outer to inner circles of the chart. Moderate evidence supported the 30 and 108 dph treatments having a faster escape mean speed and further escape distance in both*

performance temperatures compared to the control (0 dph). Strong evidence supported the 108 dph treatment turning further clockwise in both performance temperatures compared to the control (0 dph). ***A*** *and* ***B*** *N = 59 (0 dph), 59 (3 dph), 60 (7 dph), 57 (30 dph), 54 (108 dph);* ***C****-****F*** *N = 46 (0 dph), 43 (3 dph), 51 (7 dph), 47 (30 dph), 42 (108 dph).*

2.4.2 Body Size

Fish with 3, 7, and 30 days' exposure post-hatching to elevated temperature showed no strong evidence of a change in standard length or weight compared to control fish (figure 2.3). There was moderate evidence for a decline in standard length for fish exposed for 7 dph (85% CI -1.42 mm to -0.18 mm), but the effect was small with an average decline of 2%. By contrast, fish experiencing the entire 108 dph at elevated temperatures displayed strong evidence for a decline in body size (95% CI *SL* -3.95 mm to -1.42 mm; *W* -0.509 g to -0.111 g), with fish on average 7% shorter and 16% lighter than control fish (figure 2.3). In addition, there was moderate evidence for sex differences (85% CI *SL* -0.58 mm to -0.05 mm; *W* -0.105 g to -0.015 g), with males on average 1% shorter and 3% lighter than females (figure 2.3). The models explained 14% (marginal r^2) and 27% (conditional r^2) variability of standard length and 10% (marginal r^2) and 23% (conditional r^2) variability of weight. There was no evidence for a difference in sex ratios between the control and exposure duration treatments (appendix figure 2.4).

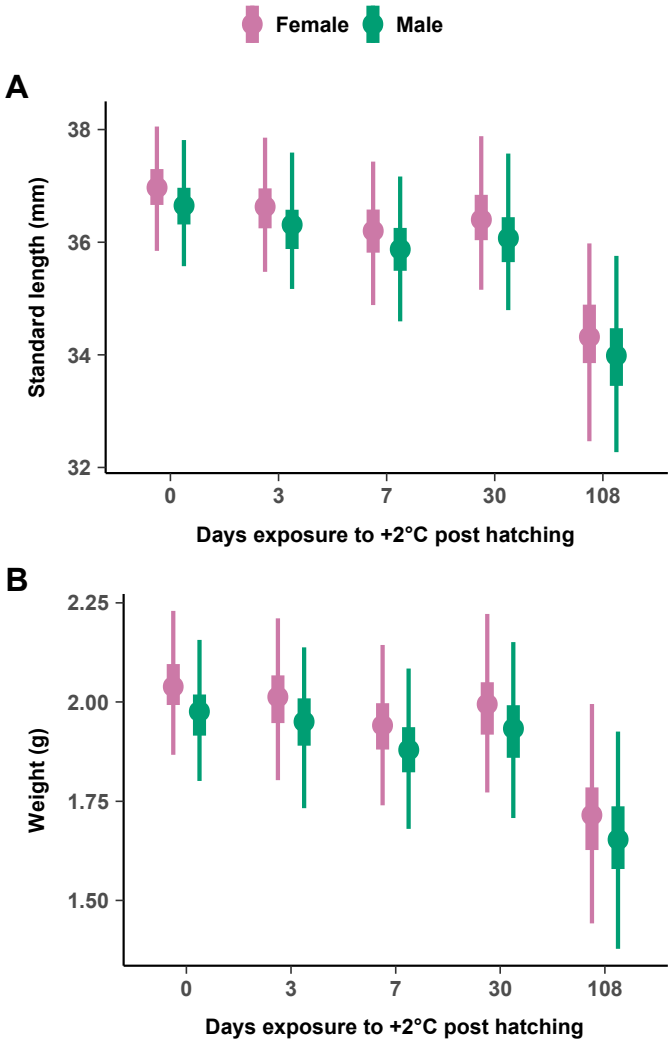

*Figure 2.3 Body size. Bayesian posterior medians (circles), 50% credible intervals (thick lines), and 95% credible intervals (thin lines) of fish **A** standard length and **B** wet weight. Strong evidence supported the 108 dph treatment being shorter and lighter compared to the control (0 dph). Moderate evidence supported males being shorter and lighter relative to females in all treatments. N = 114 (0 dph), 120 (3 dph), 120 (7 dph), 116 (30 dph), 119 (108 dph).*

2.4.3 Critical Thermal Maximum

Fish exposed to increasing lengths of warming showed no evidence of a change in CT_{max} compared to control fish (figure 2.4). Strong evidence demonstrated longer fish withstand a higher CT_{max}; however, there was an interaction because fish in the 3 dph exposure duration treatment exhibited the opposite trend (appendix figure 2.5). The model explained 21% (marginal r^2) and 61% (conditional r^2) variability of CT_{max}. Finally, there was no evidence that trial starting temperature had an influence on CT_{max} outcomes.

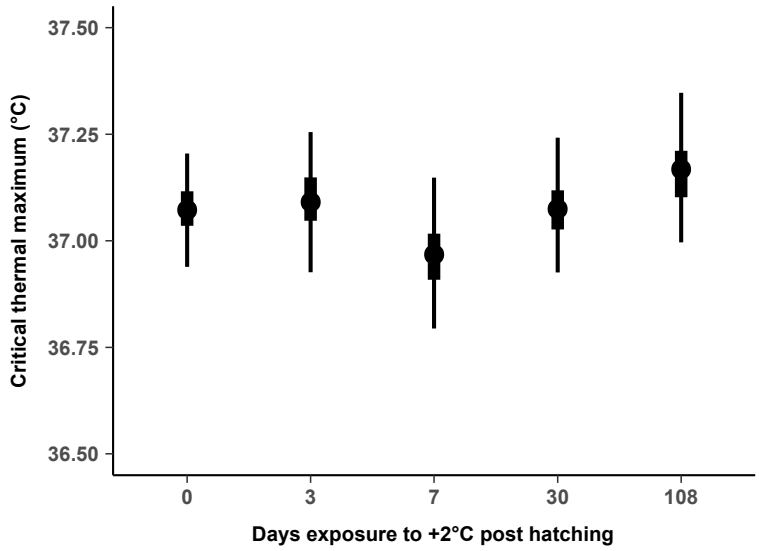

Figure 2.4 Critical thermal maximum. Bayesian posterior medians (circles), 50% credible intervals (thick lines), and 95% credible intervals (thin lines) of the critical thermal maximum held at the average standard length (35.82 mm) of fish tested. There was no evidence of a difference between the treatments. N = 24 fish per treatment.

2.4 Discussion

My results show that extended exposure to heatwave conditions, early in life, can affect ecologically important traits in juvenile reef fish. Exposure to +2°C conditions for 30 or 108 dph enhanced the mean escape speed and escape distance. Fish continuously exposed to increased temperatures (108 dph) also experienced a change in escape direction. Shorter exposure durations of 3 and 7 dph did not result in changes to escape performance, potentially indicating the length of exposure was not sufficient to cause phenotypic change. Increases in escape speed and distance away from a potential predator would likely be beneficial in a natural reef setting. Fish continuously exposed to elevated temperatures from hatching (108 dph) were substantially smaller, illustrating the potential energetic cost of ongoing exposure to warming. By contrast, fish exposed for 3, 7, and 30 dph to increased temperatures did not exhibit considerable reductions in body size. This may because the length of exposure was insufficient to have an effect on growth, or alternatively due to compensatory growth following an initial period of reduced growth during high temperature exposure (Metcalfe & Monaghan, 2001). No effect of thermal exposure duration was observed for critical thermal maximum, combined with previous work in *A. polyacanthus* this suggests a short-term physiological constraint of ~37°C in this species.

Developmental plasticity allowed fish exposed for 30 and 108 dph to simulated heatwave conditions to swim faster and further during an escape compared to fish reared at present-day control temperatures. Enhanced mean escape speed and distance in 30 and 108 dph treatment fish was observed in both of the performance temperatures, demonstrating that this was a developmental effect rather than an effect of water temperature at the time of testing. This potentially indicates the altered phenotypes were fixed in place during a critical window after 8 dph, but before 30 dph. Jarrold et al. (2018) supports this idea, as they found enhancements in escape speed, distance, and turning rate in *A. polyacanthus* reared at +2°C for 28 dph. The phenotypic change observed in 30 and 108 dph is also likely related to the length of exposure (Schulte et al., 2011) with exposure greater than 7 dph required to induce phenotypic change. Since phenotypic change is energetically costly, responding to incorrect cues would be maladaptive, thus it is likely that a certain duration of cue exposure would be required before a permanent phenotypic change is induced (Angilletta Jr, 2009). Determining the interplay between timing and length of exposure would require additional investigation; however, combining the present results with previous research on the thermal sensitivity of *A. polyacanthus* during early life suggests that juveniles remain sensitive to warming between 30 and 60 dph (Donelson et al., 2011; Rodgers et al., 2017). This implies that exposure to a heatwave during a critical window is essential to induce phenotypic change in juvenile reef fishes but that the duration of exposure may also be critical.

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

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

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

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

Fish that developed entirely at elevated temperatures were smaller than fish from all other exposure duration treatments and the control group. Smaller body size is ecologically important in juvenile fish as it typically increases the risk of predation and reduces competitive ability (Goatley & Bellwood, 2016; Poulos & McCormick, 2015; Sogard, 1997). Reduced body size is likely due to increased energy costs for maintenance activities at higher temperatures

(Munday et al., 2008; Pörtner & Knust, 2007). While no substantial differences in body size were observed when measured at the end of the experiment in fish exposed for 3, 7, or 30 dph to elevated temperature compared to present-day control fish, I cannot conclude that there was no effect of water temperature on growth during the high temperature exposure. Either the length of exposure to high temperature had no impact on their body size or there was an effect after which compensatory growth occurred. Compensatory growth is common in fish following periods of stress or reduced resource availability (Ali et al., 2003) and once more favourable conditions arise, a growth spurt occurs through recoupment of energy reserves and increased investment in structural growth (Auer et al., 2010). My results are likely due to compensatory growth, especially for fish exposed 30 dph, as I know body size is reduced with development at elevated temperatures (+1.5 to +3.0°C) in the first 15-30 days (Donelson et al., 2014). Compensatory growth may, however, come with negative consequences later in life, such as an increased metabolism (Criscuolo et al., 2008), reduced number of offspring (Auer et al., 2010), or a shortened lifespan (Lee et al., 2012). One aspect of the experimental set up that may have influenced growth to be homogeneous across thermal exposure durations is that fish were grown in groups, allowing social interactions to influence body size. Interestingly, I observed a difference in body size between the sexes, with males being 1-3% smaller than females and no sex bias observed (i.e. more males). However, this sex effect was small compared with the average effect of the treatment (7-16%).

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

simply be an artefact of different starting temperatures. My work supports the growing consensus that critical thermal maxima are not highly plastic and suggests there is a physiological constraint around 37°C in *A. polyacanthus*.

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

Chapter 3 Sex- and Time-specific Plasticity of Ocean Warming on Reproduction and Offspring Quality in a Coral Reef Fish

This chapter was published in Evolutionary Applications (2021) 14, 1145-1158, DOI:10.1111/eva.13187. Authors: Rachel K. Spinks, Lucrezia C. Bonzi, Timothy Ravasi, Philip L. Munday, and Jennifer M. Donelson.

The associated data are available on Research Data JCU repository, DOI:10.25903/5f14fa3fafaba, and the R script of analyses is available in the publication's supplementary material.

3.1 Abstract

Global warming can disrupt reproduction or lead to fewer and poorer quality offspring, owing to the thermally sensitive nature of reproductive physiology. However, phenotypic plasticity may enable some animals to adjust the thermal sensitivity of reproduction to maintain performance in warmer conditions. Whether elevated temperature affects reproduction may depend on the timing of exposure to warming and the sex of the parent exposed. I exposed male and female coral reef damselfish (*Acanthochromis polyacanthus*) during development, reproduction or both life stages to an elevated temperature (+1.5°C) consistent with projected ocean warming and measured reproductive output and newly hatched offspring performance relative to pairs reared in a present-day control temperature. I found female development in elevated temperature increased the probability of breeding, but reproduction ceased if warming continued to the reproductive stage, irrespective of the male's develop- mental experience. Females that developed in warmer conditions, but reproduced in control conditions, also produced larger eggs and hatchlings with greater yolk re- serves. By contrast, male development or pairs reproducing in higher temperature produced fewer and poorer quality offspring. Such changes may be due to alterations in sex hormones or an endocrine stress response. In nature, this could mean female fish developing during a marine heatwave may have enhanced reproduction and produce higher quality offspring compared with females developing in a year of usual thermal conditions. However, male development during a heatwave would likely result in reduced reproductive output. Furthermore, the lack of reproduction from an average increase in temperature could lead to population decline. These results demonstrate how the timing of exposure differentially influences females and males and how this translates to effects on reproduction and population sustainability in a warming world.

3.2 Introduction

Reproduction is fundamental to sustaining viable populations. Reproductive activities generally occur within a narrow subset of the organism's entire thermal range, due to the energetic costs and physiological optimisation that reproduction requires (Pörtner et al., 2006; Van Der Kraak & Pankhurst, 1997; Visser, 2008). Consequently, any changes in environmental temperature, such as human-induced warming, can disrupt reproduction or influence the quantity and quality of offspring produced (Adams, 2010; Bokhorst, Bjerke, Street, Callaghan, & Phoenix, 2011; Pankhurst & Munday, 2011). To compensate for environmental temperature change, some organisms shift their location and/or reproductive phenology so that reproduction still occurs within the thermal optima (Ling, Johnson, Frusher, & King, 2008; Poloczanska et al., 2013). However, these changes may result in a mismatch between reproduction and food availability for offspring when trophic levels are not similarly affected by temperature change (Visser & Both, 2005). Additionally, some species will be unable to shift timing or location to maintain reproduction at optimal temperatures, and instead could adjust the thermal sensitivity of reproduction through processes such as phenotypic plasticity (non-genetic effects) and/or genetic evolution (Donelson et al., 2019). If shifts in reproductive timing or location, and/or adjustments to the thermal sensitivity of reproduction are not possible, there are likely to be serious consequences for population sustainability (Visser, 2008).

Due to the rapid rate of warming projected to occur over the coming decades, phenotypic plasticity is expected to be a critical mechanism by which organisms maintain performance in warmer conditions (Hendry, Farrugia, & Kinnison, 2008; Munday, Warner, Monro, Pandolfi, & Marshall, 2013). Phenotypic plasticity allows a genotype to produce different phenotypes in different environments (Pigliucci, 2005; Stearns, 1989a), and can be adaptive or maladaptive (Ghalambor et al., 2007). Whether phenotypic plasticity occurs may depend on the timing of exposure with early periods in development most sensitive to environmental change (West-Eberhard, 2003). Environmental conditions experienced during early development can induce strong and permanent phenotypic change (i.e. developmental plasticity), whereas adult phenotypic adjustments are usually reversible (i.e. reversible plasticity) and are expected to be comparatively less sensitive (Angilletta Jr, 2009).

There is evidence that phenotypic plasticity can mediate the effects of rising temperature on traits such as aerobic physiology, growth, or behaviour (Forster, Hirst, & Atkinson, 2012; Nagelkerken & Munday, 2016; Seebacher et al., 2015); however, this means little if organisms cannot reproduce. For example, mosquitofish readily adjusted swimming speed to

increased temperatures, yet will likely struggle to reproduce as sperm ceased to function at those same high temperatures (Adriaenssens, van Damme, Seebacher, & Wilson, 2012; Wilson, 2005). Current knowledge about the effects of warming on reproduction and the potential for plasticity comes largely from research testing the potential for reversible plasticity on reproductive adults (e.g. Donelson, Munday, McCormick, Pankhurst, & Pankhurst, 2010; Fischer, Brakefield, & Zwaan, 2003; Miller, Kroon, Metcalfe, & Munday, 2015; Suckling et al., 2015; Vilchis et al., 2005). When warming has instead occurred outside of this reproductive or post-maturity period, researchers generally exposed animals to increased temperatures for their entire life, making it impossible to disentangle the effects of temperature in development versus reproduction (for exceptions see Donelson, Wong, Booth, & Munday, 2016; Fischer, Eenhoorn, Bot, Brakefield, & Zwaan, 2003; Fuxjäger et al., 2019; Huey, Wakefield, Crill, & Gilchrist, 1995; Stillwell & Fox, 2005). High temperature exposure at different life stages is especially relevant to heatwaves, which coincide with summer reproductive and early developmental windows for many organisms. Heatwaves are predicted to increase in frequency, intensity, and duration due to global warming (Frölicher et al., 2018; Perkins-Kirkpatrick & Gibson, 2017). To accurately predict responses of organisms to climate change we require a greater understanding of how warming impacts reproduction depending on the timing of exposure and the capacity for adjustment through phenotypic plasticity.

While both parents contribute to offspring phenotype, mothers are generally expected to be more important due to their ability to make non-genetic contributions via provisioning or the transfer of mitochondria (Ho & Burggren, 2010; Mousseau & Fox, 1998). However, this classic idea is often shown to be a simplistic view of maternal and paternal contributions with both parents having both a genetic (i.e. DNA) and non-genetic/epigenetic influence (e.g. methylation, non-coding RNA, or chromatin structure; Bonduriansky & Day, 2009). Furthermore, dependent on the reproductive strategy, sexes may have different capacity to adjust phenotypes, such as when only one parent provides parental care (Hunt & Simmons, 2000; Roth, Klein, Beemelmanns, Scharsack, & Reusch, 2012). For example, male stickleback fish solely care for eggs and juveniles and as such early offspring size was largely driven by paternal lifetime temperatures (Shama & Wegner, 2014; van Iersel, 1953). Whether environmental temperature experienced by parents will affect the phenotype of offspring can depend on the timing of thermal change, length of exposure, and whether both parents experience the same thermal conditions (Donelson et al., 2018). Stillwell and Fox (2005) showed hatching success in a seed beetle is dependent on the interaction of the female's developmental and oviposition temperature, yet like many other studies the effect of warming

to males is unknown. It is imperative we understand how the timing of exposure to both females and males affects reproduction and offspring performance if we are to predict the effects of warming on future population success.

Fishes are ectotherms with limited capacity for internal temperature regulation and, consequently, cellular function and physiological performance, including reproduction, are tightly linked to environmental temperature (Van Der Kraak & Pankhurst, 1997). Reproduction and embryogenesis are also the most thermally sensitive time for fishes (Dahlke, Wohlrab, Butzin, & Pörtner, 2020). Temperature can directly affect fish reproduction by promoting or inhibiting hormone synthesis, altering hormone structure, and modifying the action of hormones and enzymes in the hypothalamus, the pituitary, and the gonads, resulting in changes to gamete and offspring quantity and quality (Pankhurst & Munday, 2011). For coral reef fishes, reproduction typically occurs during spring and summer. The repercussions of a 0.5-3°C increase in average summer temperature in coral reef fishes includes reduced or disrupted breeding, limited sperm production, and fewer and smaller offspring (Donelson et al., 2010; Kokita, 2003; Miller et al., 2015). However, most of these studies test adult fish for one breeding season under elevated temperatures and thus may not capture the full potential of thermal plasticity. When the full potential for thermal plasticity was explored, exposure to elevated conditions (+1.5°C) throughout development resulted in improved reproduction and offspring performance in some traits (beneficial developmental plasticity; Donelson et al., 2014). In addition, thermal conditions during reproduction can interact with those experienced during development to affect reproduction and offspring performance (Donelson et al., 2016) with some offspring traits, for instance sex ratio, only affected by the parent's developmental temperature (Donelson & Munday, 2015). A critical aspect of understanding the effects of environmental temperature change yet to be explored is whether timing of exposure differentially affects mothers and fathers and how this influences reproduction and newly hatched offspring.

The present study explores how the ontogenetic timing of exposure to simulated ocean warming affects reproduction and newly hatched offspring performance, and whether warming differentially affects mothers and fathers. For this study I used the common coral reef damselfish, *Acanthochromis polyacanthus*. Specifically, male and female damselfish were reared from hatching in either a present-day temperature (control) or an elevated temperature (+1.5°C). Once mature (1.5 years), fish were subsequently divided orthogonally into control and elevated reproductive temperatures to create pairs such that every thermal combination of sex

and time (development, reproduction, or both life-stages) occurred (8 pair combinations). A broad range of reproductive and hatchling traits were measured. This experimental design allows estimation of the relative non-genetic maternal and paternal contributions, exposure timing effects and their interactions. I also tracked family origins to estimate genetic effects. Since *A. polyacanthus* lack a dispersal larval stage, adults are site attached with small home-ranges and breeding pairs are monogamous (Miller-Sims et al., 2008; Robertson, 1973), temporal environmental variation is most likely to explain why a mother and father from the same pair have different developmental thermal histories or one pair experiences a different developmental or reproductive temperature from another pair. I hypothesised that parental developmental exposure to elevated temperature would benefit reproductive and hatchling traits, but reproduction in elevated temperature alone would result in negative effects. This is because *A. polyacanthus* appears to have limited capacity as an adult to adjust to warming in comparison to during development (Chapter 2; Donelson et al., 2011, 2010; Rodgers et al., 2018). Lastly, I expected female developmental exposure to higher temperature would have the greatest influence on reproductive traits, because of her larger initial investment (i.e. eggs), but both sexes would have a similar influence on hatchling traits since this species exhibits joint parental care.

3.3 Methods

3.3.1 Experimental Design

In the present study we used the spiny chromis damselfish, *A. polyacanthus* (Bleeker 1855), which is common on coral reefs in the Indo-Australian archipelago. Adult *A. polyacanthus* form monogamous pairs and breed primarily during the summer months (Robertson, 1973). Egg clutches adhere to the substrate with joint parental care and direct development taking place (Kavanagh, 2000; Pankhurst, Hilder, & Pankhurst, 1999). Adult fish (F0 generation) were collected from the Palm Islands region (18° 37′ S, 146° 30′ E) of the central Great Barrier Reef in 2014 and 2015. Fish were transported to the Marine and Aquaculture Research Facility at James Cook University, Townsville, Australia, and housed in breeding pairs within 60 L aquaria, each with half a terracotta pot as a spawn site. Pairs were kept at seasonally cycling, present-day temperatures approximating the Palm Islands region (AIMS, 2016). In the Austral summer of 2016, breeding bouts from six wild-caught pairs were used in this experiment. Egg clutches were kept with the parents until hatching, allowing them to provide nest care as occurs in the wild.

The F1 generation was maintained in a 25,000 L recirculating system supplied with a continuous flow of natural seawater with precise temperature control. The system was divided into six blocks, each with its own sump, independent temperature control and approximately 40 42L opaque tanks (6×2 kW Control Distributions custom-built heaters, Carlton, NSW, Australia; 18 kW Solarwise chiller EXC341RC, Kingston, QLD, Australia). Water and air temperature were monitored continuously from a centralised environmental control system (PR Electronics temperature transmitter 5333A, ±0.1°C, Rønde, Denmark; Innotech Genesis II controller V5, Brisbane, QLD, Australia) and manually verified daily with a digital thermometer (±0.1°C, C26, Comark Instruments, Norwich, Norfolk, UK). Salinity, pH, and nitrates were measured fortnightly and maintained around 35 ppm, 8.1 and below 20 mg/l, respectively. Water quality was maintained with mechanical, biological, and ultraviolet filtration, protein skimming, and partial water changes. An elevated temperature of +1.5°C was selected to match sea surface temperatures projected to occur on the Great Barrier Reef by 2050 – 2100 (IPCC, 2013) and to allow comparison with previous research on reproduction in similar populations (Donelson et al., 2014, 2010, 2016). This realistic average temperature increase already occurs during marine heatwaves (Chapter 2; Frölicher et al., 2018). The control water temperature simulated seasonal (winter minimum 23.2°C, summer maximum 28.5°C) and diurnal (0300 hrs -0.6°C, 1500 hrs +0.6°C) cycles for the Palm Islands region based on temperature loggers from 2002 to 2015 at 0.2-14.6 m depth (AIMS, 2016), with the elevated treatment matching this but 1.5°C higher (figure 3.1). Similarly, the photoperiod of the Palm Islands region was replicated, reaching a maximum of 13h 15m light in summer (December) and a minimum of 11h 01m light in winter (June). Seasonal changes to water temperature and illumination were adjusted weekly.

In the Austral summer of 2016, newly hatched siblings (F1 generation) were split to be reared in a present-day control temperature or +1.5°C (figure 3.1). For each of the six families, fish were randomly allocated within six hours of hatching to a minimum of five replicate tanks at each temperature, with approximately 10 fish per tank. Fish were given 2-3 hours to slowly equilibrate to their rearing temperature via a 2 L tub floated in the tank and receiving a gradual inflow. At approximately eight months of age, fish were sexed via external examination of the urogenital papilla (Hilder & Pankhurst, 2003) and permanently marked with colour elastomer tags (Northwest Marine Technology, Shaw Island, WA, USA) to track developmental temperature, sex, and family line without further disturbance. By one year of age, fish were placed in sibling pairs to reduce competitive fighting. In the late Austral winter of 2017, when fish were approximately 1.5 years of age (i.e. maturation), all groups were adjusted to 24.5°C (±0.6°C diurnal variation) over a period of one week. This was to create non-sibling breeding

pairs in preparation for the Austral summer breeding season of 2017/2018 (when fish were ~2 years old). The 24.5°C pairing temperature was a 1.3°C increase and a 0.2°C decrease from minimum winter temperature in the control and elevated temperature treatments, respectively. The breeding design included reciprocal sex crosses of the developmental temperatures resulting in four pair combinations of males and females reared in present-day control and elevated temperatures, following figure 1A in Bonduriansky, Crean, and Day (2012). The four pair combinations were further divided into present-day control and +1.5°C reproductive temperatures, which resulted in eight pair combinations (figure 3.1). The eight pair combinations were replicated at least 20 times across three family crosses (family A×C, family B×D, family E×F) from the original six F0 families (see figure 1A Bonduriansky et al., 2012). After four weeks of pairing, I gradually adjusted the fish to early spring temperatures over two weeks and re-established the 1.5°C difference so that the control reproductive pairs were at 25.5°C ±0.6°C and the elevated reproductive pairs were at 27°C ±0.6°C by late September. Pairs were provided half a terracotta pot as a spawn site.

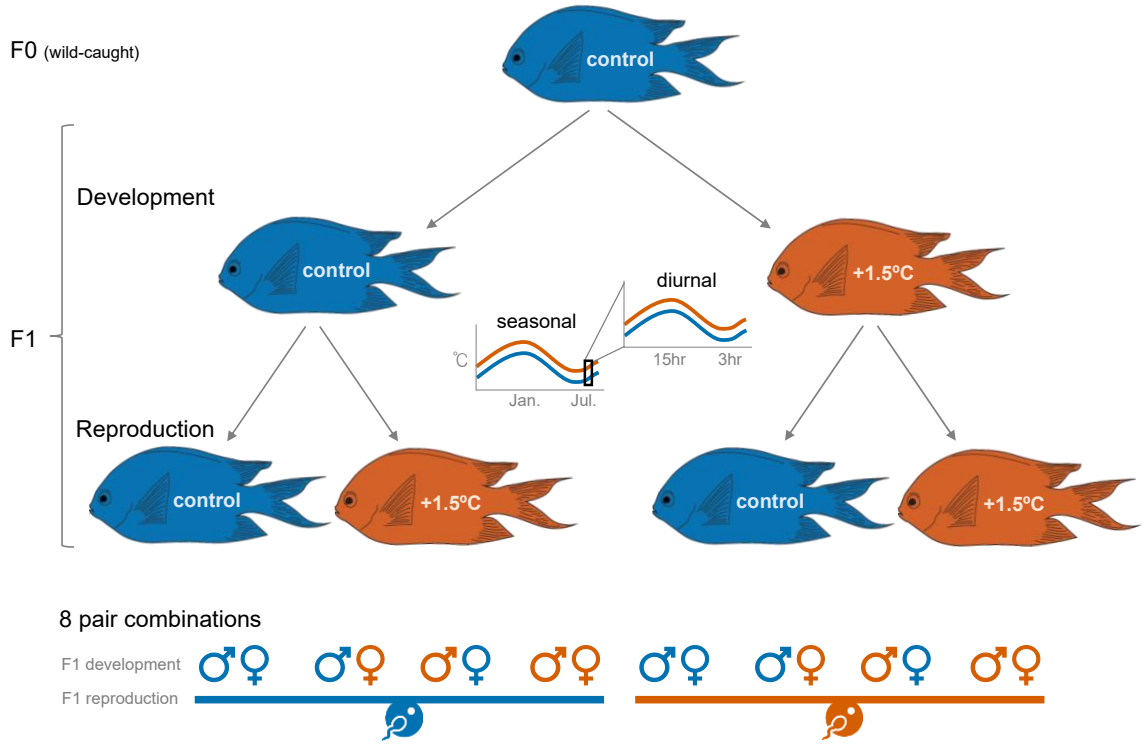

Figure 3.1 Experimental design. The F1 developmental split occurred shortly after hatching and the F1 reproductive split occurred at 1.5 years. Blue represents the present-day control temperature (in summer 28.5°C with ±0.6°C diurnal variation), orange represents a temperature increase of 1.5°C (in summer 30.0°C with ±0.6°C diurnal variation).

Newly hatched *A. polyacanthus* were fed live *Artemia nauplii* the first three days then weaned to 200–400 µm NRD pellets (INVE Aquaculture Salt Lake City, UT, USA) supplied daily at 5.18mg/fish and from 46 days post hatching (dph) at 21.7mg/fish. Between 96 dph and 300 dph 500–800 µm NRD pellets were supplied daily initially at 29.29 mg/fish and then increased to 58.56 mg/fish. After this period *A. polyacanthus* were given G12 adult breeder pellets at least once per day until satiation.

3.3.2 Reproduction and Offspring Traits

Summer temperatures were reached on the 8th of November 2017 and maintained until the last clutch hatched in May 2018 (28.5°C with ±0.6°C diurnal variation for control and 30.0°C with ±0.6°C diurnal variation for elevated reproductive temperatures). Tanks were checked daily for

the presence of eggs. I calculated the probability of breeding during summer temperatures from pairs that had a minimum of six weeks together as this would indicate a stable pairing. When an egg clutch was discovered, an underwater photograph was taken (Canon G16 camera & housing; Tokyo, Japan) to determine the number of eggs laid. Clutch size for each pair was calculated from the first egg clutch photographed once summer temperature was reached, hereafter referred to as the first clutch. In 11 cases pairs laid a clutch prior to the onset of summer temperatures. The total eggs per pair laid were summed from a maximum of two clutches. We could not calculate beyond two clutches as several pairs were sacrificed at this point for molecular research. Also, *A. polyacanthus* typically lay just 1-2 clutches per year in the wild (Thresher, 1985), so these first two clutches are ecologically relevant. For the total eggs laid calculation I only included pairs that stayed together at least six weeks since their first clutch hatched. Once the first clutch was photographed, 10 eggs were sampled from random locations within the clutch and photographed to determine egg area (±0.01 mm^2). Clutches were kept with the parents allowing them to provide nest care as occurs in the wild. On day eight, the first clutch was photographed again to determine embryonic mortality. Eggs no longer present (most likely removed by parents) or that had not developed were considered deceased. Embryonic duration was estimated from the first clutch beginning the day it was laid until it hatched. Within hours of hatching, 20 offspring from each clutch were euthanised by an overdose of clove oil. They were weighed (±0.1 mg; excess water removed with a Kimwipe) and then preserved in phosphate buffered formaldehyde (4%) to photograph within 48 hrs to determine hatch standard length (±0.01 mm) and hatch yolk area (±0.01 mm^2). I was unable to measure the standard length of 4 hatchlings or yolk area of 7 hatchlings due to mishandlings after weighing. Clutch size at laying and day eight, egg area, hatch standard length, and hatch yolk area were measured blind by the same person (B. Spady) using ImageJ software v. 1.50i (Schneider et al., 2012). This research was conducted under James Cook University's animal ethics approval A1990, A2210, and A2315.

3.3.3 Statistical Analyses

I used the rstanarm package v.2.18.2 (Goodrich et al., 2020) to implement Bayesian mixed models. I tested whether reproductive and offspring performance for the pairs with various sex and life-stage exposures to warming differed compared to pairs exposed their entire lives to present-day control temperature. The F1 thermal experience (♂♀, ♂♀, ♂♀, ♂♀, ♂♀, ♂♀, ♂♀, ♂♀, ♂♀) was an independent variable in all models, with the control group set as the

intercept (♂♀). The intercept varied by male family and female family to prevent pseudoreplication and so the variance attributed to paternal and maternal family-level effects could be estimated (Arnqvist, 2019). Additionally, the intercept varied by pair replicate, defined as pairs from the same family cross within treatments, to prevent pseudoreplication (Arnqvist, 2019). For the dependent variables: egg area, embryonic mortality, hatch weight, standard length, and yolk area; where multiple eggs or hatchlings came from a pair within a group of pairs from the same family cross and treatment, the intercept varied by pair nested in pair replicate. This was in addition to male and female family. Again, this 'random' effects structure prevented pseudoreplication (Arnqvist, 2019) and accounted for the hierarchical nature of the experimental design. I further explored whether both slopes and intercepts varied (i.e. random-slope random-intercept model) in egg area, embryonic mortality, hatch weight, standard length, and yolk area since they had a larger sample size. Based on visual inspection and Bayesian leave-one-out information criterion (LOOIC; Vehtari et al., 2017), hatch weight and yolk area slopes differed between the dependent variable and the F1 treatments (i.e. a full random-slope random-intercept model fitted best). Variances attributed to 'random' effects are always stated in the model link scale.

The dependent variables egg area, embryonic duration, hatch weight, hatch standard length, and hatch yolk area were modelled with a Gaussian distribution and an identity link (i.e. LMM). Embryonic duration is a count and therefore a Poisson distribution is normally expected, but due to underdispersion I found a Gaussian distribution with narrow priors provided the best fit. It was possible to use a Gaussian distribution here because no relationship existed between the mean and variance and means did not approach zero. The dependent variables clutch size and total eggs per pair being counts were modelled with a Poisson distribution and a log link (i.e. GLMM). To manage overdispersion in these Poisson models I included observation-level random effects, where each data point (i.e. pair) receives a unique level of a random effect (Harrison, 2014). I found observation-level random effects were a better solution visually and via LOOIC than using a negative Binomial distribution. Observation-level random effects were excluded in conditional R^2 calculations as in this circumstance it has little biological meaning (Harrison, 2014). Lastly, the dependent variables breeding probability and embryonic mortality were modelled with a Binomial distribution and logit link (i.e. GLMM) due to their binary properties.

Mother size was initially considered a covariate for the dependent variables clutch size, total eggs per pair, and egg area because they often correlate (Lim, Senior, & Nakagawa, 2014).

However, I found no clear correlations and model fits visually and via LOOIC improved when excluding mother size. This may be due to mother size measurements being taken at different time points (most females were measured at the end of the breeding season to prevent disturbance, but some were measure when euthanised for molecular research), or because of limited size differences as all fish were the same age. The general conclusions were the same with and without mother size and no interactions were present so we selected the most parsimonious models.

Bayesian models allow integration of prior knowledge (Kruschke, 2015). I specified weakly informative priors using rstanarm except when a more informative prior was required to allow regularisation, or because specific knowledge existed (appendix table 3.1; Donelson et al., 2014, 2010, 2016). The posterior distribution is derived from the prior distribution (previous evidence) and the likelihood function (new evidence). Visual posterior checks confirmed that priors never heavily influenced the posterior. Using the Hamiltonian Monte Carlo algorithm, models were run with three chains by means of the No-U-Turn sampler for a minimum of 5000 iterations with every second or third posterior sample thinned and the first 10-50% discarded depending on the complexity of the model. Model validation and selection followed Chapter 2. The probability that a treatment was smaller or larger relative to the control group is calculated from the posterior distribution. Probabilities are expressed as a percent and the closer they are to 100% suggests greater confidence in a treatment being smaller or larger relative to the control group, whereas nearer to 50% suggests little confidence in a treatment being smaller or larger relative to the control group. Highest posterior density credible intervals (analogous to Frequentist confidence intervals) are used in all figures. Analyses were performed in R v.3.6.0 (R Core Team, 2020) with figures created in the ggplot2 package v.3.1.1 (Wickham, 2016).

3.4 Results

Pairs comprised of a male and female that developed and reproduced at control temperature (♂♀) had a 34% median breeding probability (figure 3.2). By contrast no pairs bred when both males and females were exposed to elevated temperature during their developmental and reproductive stages (♂♀), resulting in a 99.98% probability of fewer breeders compared to pairs exposed their entire lives to control temperature (figure 3.2). Similarly, pairs only bred once when males were exposed to control developmental temperature, females exposed to higher developmental temperature, and reproduction occurred at higher temperature (♂♀; 31% median decrease in breeding probability), with a 98% probability of fewer breeders

compared to pairs exposed their entire lives to control temperature (figure 3.2). By contrast, there was a 24% median increase in breeding probability for pairs where males developed at control, females developed at high temperature, and reproduction occurred at control temperature (♂♀), resulting in an 85% probability of more breeders than when females also developed at control temperature (figure 3.2). In all other treatments (♂♀, ♂♀, ♂♀ , ♂♀), the breeding probability was similar to that of pairs where male, female, and reproduction were in control temperature (figure 3.2; appendix table 3.2). The variance observed in breeding probability was partly due to some pair replicates breeding and others not ('random' effect pair replicate σ 1.20 log odds); however, this was generally smaller than the magnitude of treatment effects (♂♀ -17.87, ♂♀ -2.86, ♂♀ 1.03 log odds). Family effects contributed the least variance to breeding probability with the among male family standard deviation (0.57 log odds) less than female family (0.68 log odds). Further analyses of reproductive and hatchling traits exclude the treatment where males developed at control temperature, females developed at elevated temperature, and reproduction occurred at elevated temperature (♂♀) because of the uncertainty around a sample size of one and the exceptionally high embryonic mortality (74%) experienced by this clutch.

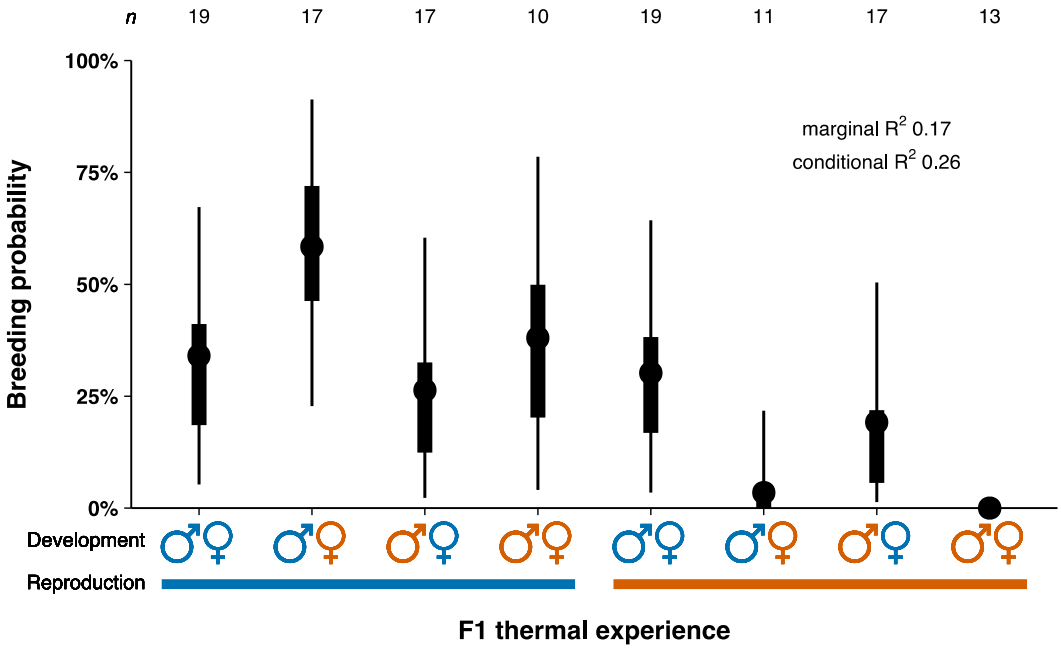

Figure 3.2 Breeding probability. Bayesian posterior median values (circles), 50% credible intervals (rectangles), and 95% credible intervals (thin lines) of the breeding probability, n = *pairs. Blue represents the present-day control temperature while orange represents a temperature increase of 1.5°C.*

Clutch size and total eggs laid per pair decreased when fathers or both parents were exposed to higher temperature during development, or when pairs were exposed to higher temperature during reproduction. Clutch size was similar across treatments except for pairs where both sexes developed at increased temperature but reproduced at control temperature (♂♀; figure 3.3A; appendix table 3.2). These pairs had a 96% probability of producing smaller clutches and a median of 87 fewer eggs per clutch compared to pairs exposed their entire lives to control temperature (figure 3.3A; appendix table 3.2). Family effects provided minimal variance to clutch size compared to the magnitude of the treatment effect (♂♀ -0.31 log), with the among male family standard deviation (0.01 log) less than female family (0.02 log). Since pairs where both sexes developed in higher temperature but reproduced in control temperature (♂♀) laid smaller clutches, it was not surprising that they also produced a median of 224 fewer eggs in total over the breeding season, resulting in a 94% probability of less eggs laid relative to pairs exposed their entire lives to control temperature (figure 3.3B; appendix table 3.2). By contrast, three treatments (♂♀, ♂♀ , ♂♀) produced similar size clutches, but laid fewer total eggs per pair due to approximately half the pairs in these treatments producing only one

clutch. A median of 245 fewer eggs in total were laid by pairs comprised of a male reared in elevated temperature, a female reared in control temperature, and reproduction in control temperature (♂♀🔵), resulting in a 96% probability of less eggs laid relative to pairs exposed their entire lives to control temperature (figure.3.3B; appendix table 3.2). When reproduction occurred at elevated temperature (♂♀🟠), a median of 322 fewer eggs in total were laid and a 97% probability of less eggs produced compared to pairs exposed their entire lives to control temperature (figure 3.3B; appendix table 3.2). For pairs where both sexes developed in control temperature but reproduction occurred at higher temperature (♂♀🟠) there was a median of 142 fewer eggs laid in total, resulting in an 84% probability of less eggs produced relative to pairs exposed their entire lives to control temperature (figure 3.3B; appendix table 3.2). Finally, pairs comprised of males reared in control temperature, females reared in increased temperature, and reproduction in control temperature (♂♀🔵) produced similar total number of eggs to that of pairs where males, females, and reproduction were in control water temperature (figure 3.3B; appendix table 3.2). Family effects provided minimal variance to the total number of eggs laid compared to the magnitude of treatment effects (♂♀🔵 -0.45, ♂♀🔵 -0.41, ♂♀🟠 -0.23, ♂♀🟠 -0.63 log), with the among male family standard deviation (0.04 log) less than female family (0.06 log).

Egg area increased slightly when females developed in warmer waters, yet decreased if males developed and reproduced at higher temperature. Pairs comprised of males in control temperature, females in elevated temperature, and reproduction in control temperature (♂♀🔵) had a median increase in egg area of 0.23 mm^2 and 83% probability of larger eggs relative to pairs exposed their entire lives to control temperature (figure 3.3C; appendix table 3.2). Conversely, pairs comprised of males in warmer water, females in control temperature, and reproduction in warmer water (♂♀🟠) had a median decrease in egg area of 0.49 mm^2 and 96% probability of smaller eggs relative to pairs exposed their entire lives to control temperature (figure 3.3C; appendix table 3.2). Egg area in all other treatments (♂♀🔵, ♂♀🔵 , ♂♀🟠) was similar to pairs exposed their entire lives to control temperature (figure 3.3C; appendix table 3.2). The variance observed in egg area was moderately explained by the 'random' effects, i.e. male family, female family, and pair nested in pair replicate (see marginal vs conditional R^2 figure 3.3C). Specifically, the largest contributor of variance was pair (σ 0.14 mm^2) although this was smaller than the magnitude of treatment effects, meaning egg area varied between pairs but we could still observe differences due to the F1 thermal experience. Conversely, family provided the least variance to egg area with the among male family standard deviation (0.03 mm^2) slightly less than female family (0.05 mm^2).

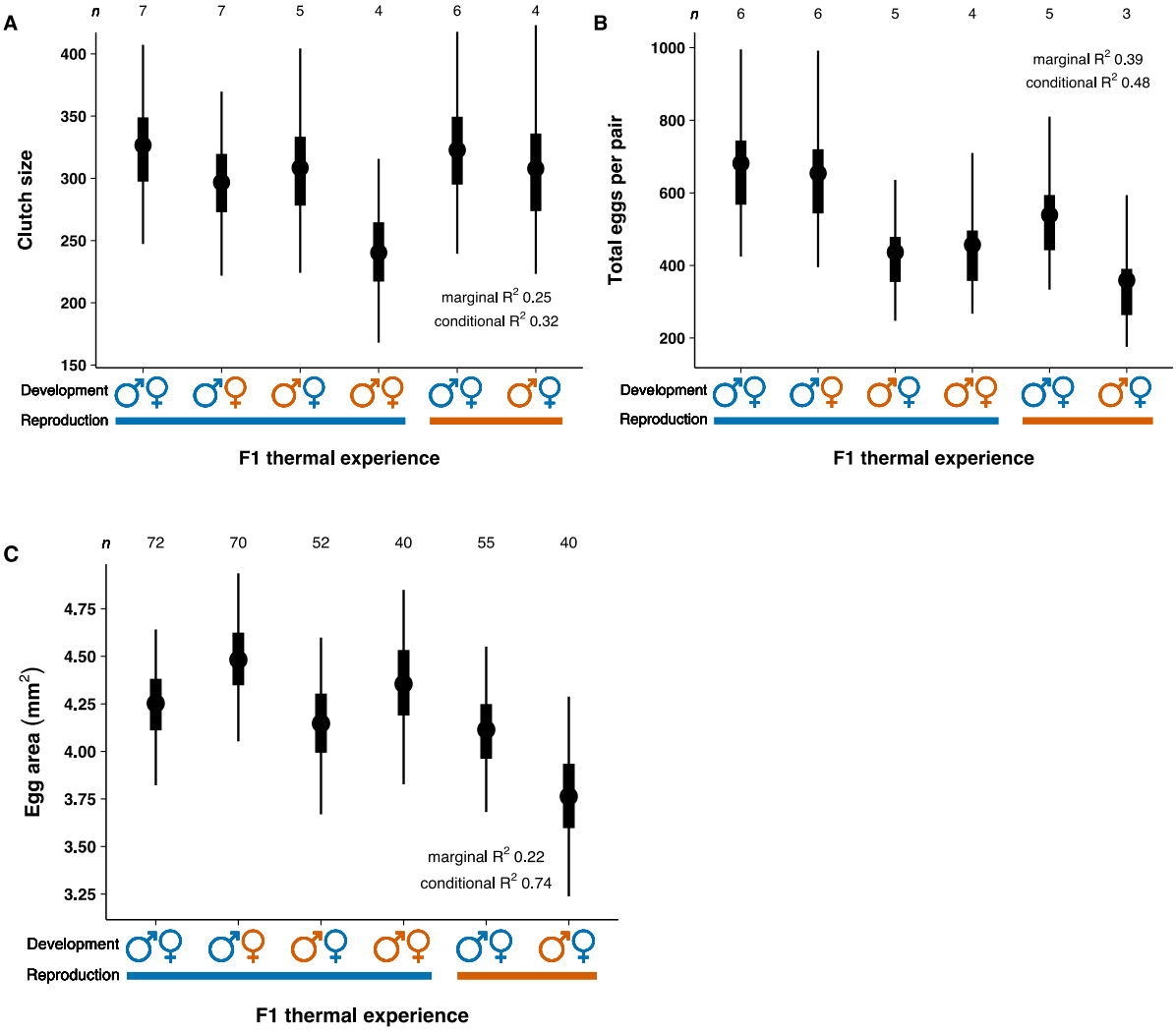

Figure 3.3 Reproductive traits. Bayesian posterior median values (circles), 50% credible intervals (rectangles), and 95% credible intervals (thin lines) of A) clutch size, n = *pairs, B) total eggs per pair,* n = *pairs C) egg area,* n = *eggs. Blue represents the present-day control temperature while orange represents a temperature increase of 1.5°C.*

Embryonic duration depended on parental exposure, whereas embryonic mortality was mostly explained by among pair variation. Embryonic duration reduced from 9 days (control ♂♀) to 8 days when the parents' reproductive temperature was elevated, irrespective of the parents' developmental environment (♂♀ and ♂♀; figure 3.4A). The probability of a shorter embryonic duration for offspring of ♂♀ and ♂♀ was 99.8% and 99% compared to parents exposed their entire lives to control temperature (figure 3.4A; appendix table 3.2). Pairs comprised of males reared in higher temperature, females reared in control temperature, and reproduction in control temperature (♂♀) and pairs where females also developed in higher

temperature (♂♀🔵) experienced an increase in their offspring's embryonic duration by half a day with a 89% and 96% probability of a longer embryonic duration relative to parents exposed their entire lives to control temperature (figure 3.4A; appendix table 3.2). The embryonic duration of ♂♀🔵 was similar to control pairs (figure 3.4A; appendix table 3.2). Family provided the least variation to embryonic duration compared to the magnitude of treatment effects, with the among male family and female family standard deviation equalling 0.04 days. Conversely embryonic mortality, which ranged from 4-13% median mortality, was largely explained by the 'random' effects, i.e. male family, female family, and pair nested in pair replicate (see marginal vs conditional R^2 figure 3.4B, appendix table 3.2). Specifically, the among pair standard deviation (4.85 log odds) was greater than the magnitude of the largest treatment effect (♂♀🟠; 1.15 log odds), meaning that embryonic mortality varied substantially between pairs making it difficult to determine differences solely due to the F1 thermal experience.

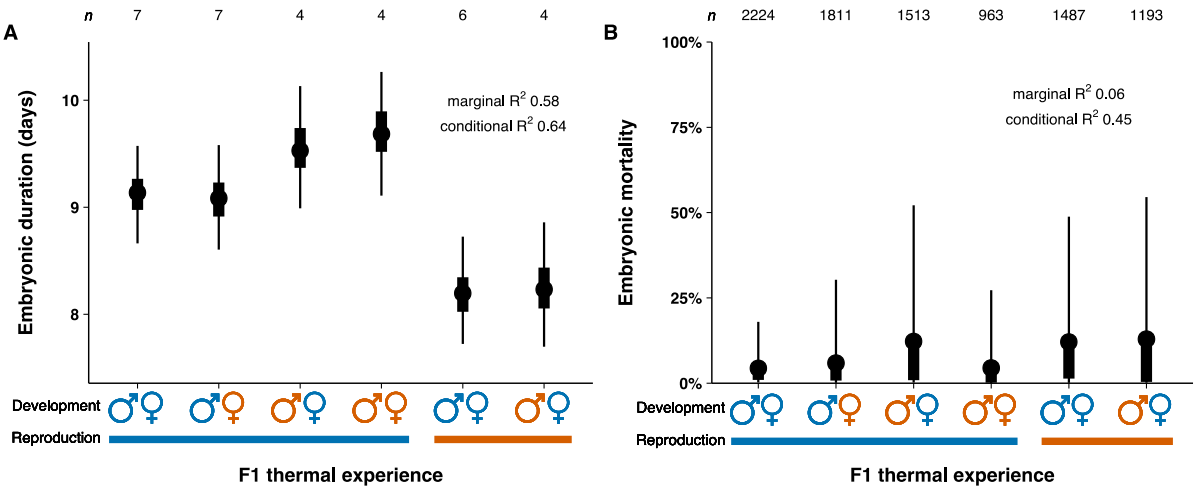

Figure 3.4 Embryonic traits. Bayesian posterior median values (circles), 50% credible intervals (rectangles), and 95% credible intervals (thin lines) of the A) embryonic duration, n = clutches and B) embryonic mortality, n = eggs. For logistical reasons (and as in the wild) offspring were kept with their parents until hatching. This meant embryos developed at their parents' reproductive temperature. Blue represents the present-day control temperature (in summer 28.5°C with ±0.6°C diurnal variation), orange represents a temperature increase of 1.5°C (in summer 30.0°C with ±0.6°C diurnal variation).

Weight at hatching decreased when parents were exposed to higher reproductive temperature. Pairs comprised of a male and female developed in control temperature and reproduced in elevated temperature (♂♀🔥) produced hatchlings that weighed a median of 0.2 mg less and an 82% probability of weighing less compared to offspring from parents exposed their entire lives to control temperature (figure 3.5A; appendix table 3.2). Pairs where males also developed at elevated temperature (♂♀🔥) similarly produced offspring that weighed a median of 0.5 mg less with a 93% probability of weighing less compared to offspring from parents exposed their entire lives to control temperature (figure 3.5A; appendix table 3.2). The rest of the treatments (♂♀❄, ♂♀❄, ♂♀❄) produced offspring similar in hatch weight to offspring from parents exposed their entire lives to control temperature (figure 3.5A; appendix table 3.2). The variance observed in hatch weight was moderately explained by the 'random' effects, i.e. father family, mother family, and F1 pair nested in F1 pair replicate (see marginal vs conditional R^2 figure 3.5A). Specifically, the largest contributor of variance was F1 pair (σ 0.04 mg) although this was smaller than the magnitude of treatment effects, meaning hatch weight varied between pairs but I could still observe differences due to the F1 thermal experience. Family effects

provided a similar amount of variance to hatch weight, with the among father family standard deviation (0.03 mg) much greater than mother family (<0.001 mg).

Standard length at hatching decreased when parents were exposed to elevated reproductive temperature. Pairs comprised of a male and a female developed in control temperature but reproduced in higher temperature (♂♀🔥) produced hatchlings that were a median of 0.24 mm shorter and a 97% probability of shorter length compared to offspring from parents exposed their entire lives to control temperature (figure 3.5B; appendix table 3.2). While there was a small decrease in hatch standard length for ♂♀❄ (-0.13 mm and 83% probability), this and the other treatments (♂♀❄, ♂♀❄, ♂♀🔥) produced offspring similar in length to offspring from parents exposed their entire lives to control temperature (figure 3.5B; appendix table 3.2). The variance observed in hatch standard length was moderately explained by the 'random' effects, i.e. father family, mother family, and F1 pair nested in F1 pair replicate (see marginal vs conditional R^2 figure 3.5B). Specifically, the largest contributor of variance was father family and mother family (σ 0.03 mm for each) although this was smaller than the magnitude of treatment effects, meaning hatch standard length varied between father families and between mother families, but I could still observe differences due to the F1 thermal experience.

Yolk area at hatching increased when mothers developed at higher temperature, irrespective of the father's developmental temperature. Pairs where males developed in control conditions, females developed in higher temperature, and reproduction occurred in control conditions (♂♀❄) produced newly hatched offspring with a median of 0.22 mm^2 more yolk and a 99.3% probability of increased yolk area compared to offspring from parents exposed their entire lives to control temperature (figure 3.5C; appendix table 3.2). Pairs comprised of a male and a female reared in higher temperature and with reproduction occurring in control temperature (♂♀🔥) similarly produced newly hatched offspring with a median of 0.24 mm^2 more yolk and a 99% probability of increased yolk area compared to offspring from parents exposed their entire lives to control temperature (figure 3.5C; appendix table 3.2). While a slight increase in hatch yolk area for ♂♀❄ (0.07 mm^2 and 79% probability) and ♂♀🔥 (0.09 mm^2 and 83% probability) was observed, these and ♂♀🔥 produced newly hatched offspring with yolks closer in size to that of parents exposed their entire lives to control temperature (figure 3.5C; appendix table 3.2). The variance observed in hatch yolk area was moderately explained by the 'random' effects, i.e. father family, mother family, and F1 pair nested in F1 pair replicate (see marginal vs conditional R^2 figure 3.5C). Specifically, the largest contributor of variance was pair

(σ 0.005 mm^2) although this was smaller than the magnitude of treatment effects, meaning hatch yolk area varied between F1 pairs but I could still observe differences due to the F1 thermal experience. Family provided the least variation to hatch yolk area with the among father family and mother family standard deviation equal (0.002 mm^2).

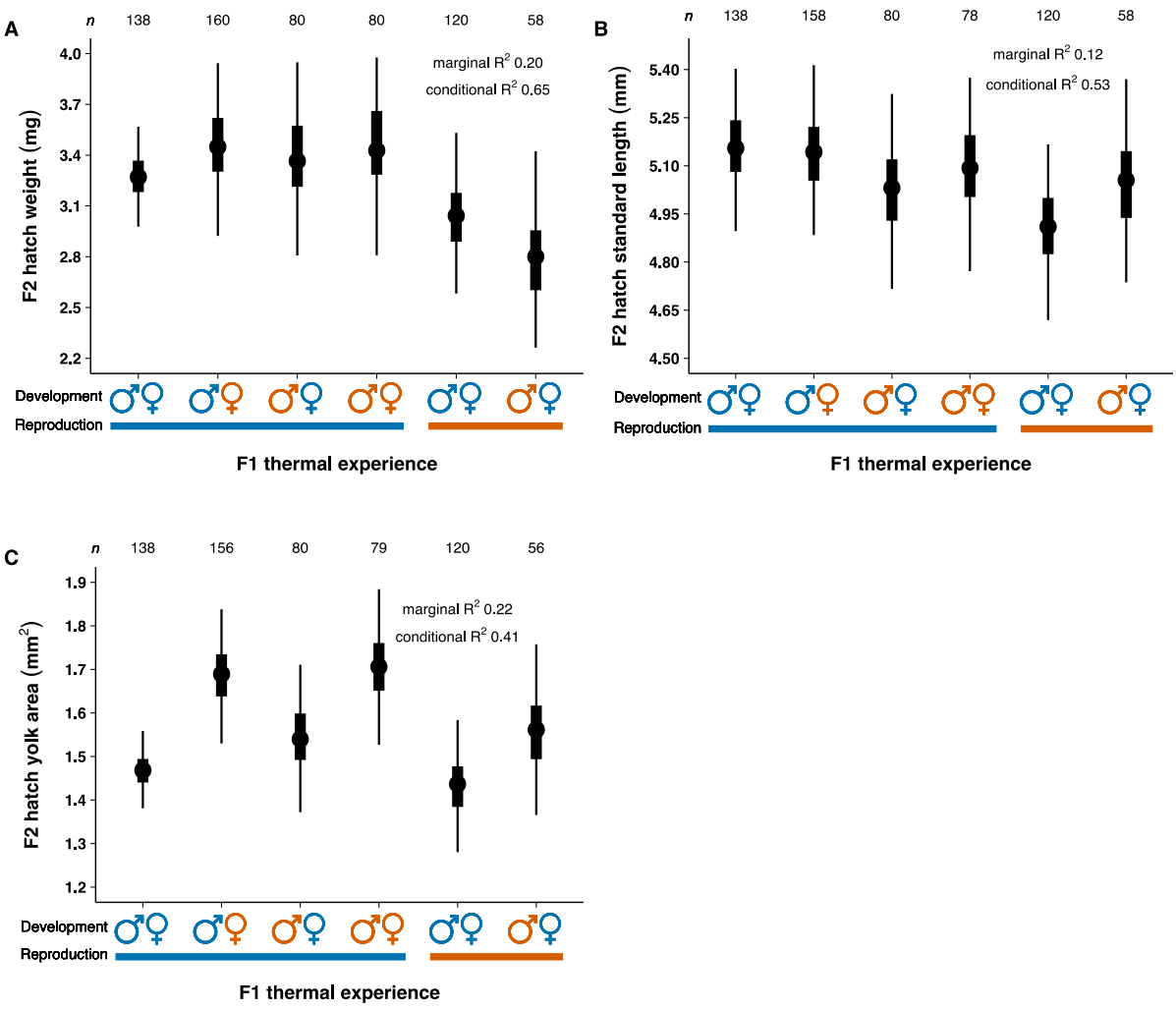

Figure 3.5 Hatchling traits. Bayesian posterior median values (circles), 50% credible intervals (rectangles), and 95% credible intervals (thin lines) of A) weight, B) standard length, and C) yolk area at hatching, n = *hatchlings. Blue represents the present-day control temperature while orange represents a temperature increase of 1.5°C.*

3.5 Discussion

Successful reproduction is vital to ensure the persistence of populations and species. Our results show that the ontogenetic timing of exposure to a 1.5°C increase in water temperature influenced fecundity and hatchling performance in a coral reef fish, and these impacts differed depending on the sex of the parent exposed. Specifically, developmental exposure to warming by females enhanced reproduction and offspring quality, whereas developmental exposure by males reduced reproductive output. When both sexes developed in warm water, I observed a combination of the effects for male and female development. Reproduction only, or the

combination of developmental and reproductive exposure to elevated temperature by either or both sexes had negative consequences on reproductive output and offspring quality. While female development in warm water may improve reproductive performance at current-day temperature, all other combinations of exposure to warming resulted in fewer and/or poorer quality offspring or disrupted reproduction, which could lead to population decline. Our results highlight the complexity of predicting the effects of ocean warming on a population since thermal effects to reproduction interact across life stages and sexes. They also show that some species may lack the ability for plasticity to maintain reproductive performance in a rapidly warming climate. In a climate change context, heatwaves could generate a mismatch in developmental temperatures by males or females from one cohort or year breeding with fish from another cohort or year that weren't exposed to a heatwave. Heatwaves could also result in fish experiencing higher temperatures during development, but not at reproduction.

Developmental exposure of females to increased temperature enhanced some reproductive and offspring characteristics. When only females developed in warmer conditions, and reproduction occurred in control conditions, more pairs reproduced, larger eggs were laid, and hatchlings had larger yolks in comparison to pairs in control conditions. The obvious benefit being that more pairs breeding increases the total number of offspring produced, whilst progeny developing from large eggs or hatchlings with large yolks may grow faster, attain greater size, and are more likely to survive (Bagenal, 1969; Brooks, Tyler, & Sumpter, 1997; Fox, 1994; Meekan et al., 2006). Our results are in contrast to research where higher female developmental temperature resulted in smaller eggs in butterflies (Fischer, Eenhoorn, et al., 2003), lower lifetime fecundity in seed beetles (Stillwell & Fox, 2005), or lower mating success in stickleback fish (Fuxjäger et al., 2019). The reproductive changes observed in *A. polyacanthus* were likely the result of developmental plasticity of the female's endocrine system, perhaps shifting the thermal optimum for reproductive functioning. Changes to gene expression levels have previously been observed in female *A. polyacanthus* that developed at an elevated temperature (+3°C), with higher expression of the Cyp11b1 gene measured in the ovaries compared to fish reared at control temperature (Veilleux, Donelson, & Munday, 2018). The encoded protein of Cyp11b1 converts testosterone to the active metabolite 11-ketotestosterone, although mostly used by male fishes 11-ketotestosterone has been shown to accelerate development of the ovaries in cod and eels (Borg, 1994; Kortner, Rocha, & Arukwe, 2009; Lokman et al., 2002; Sudo et al., 2012). Accordingly, female *A. polyacanthus* reared in warmer water may experience rapid development of their ovaries such that they are better prepared

when reproduction occurs at control temperature for that first breeding season compared to females reared in control temperature.

Developmental exposure of males to increased temperature decreased reproductive output. When only males developed at higher temperature and then pairs reproduced at control conditions, fewer clutches were produced and embryonic durations increased. Interestingly, reduced expression of follicle-stimulating hormone receptor (Fshr) and luteinizing hormone receptor (Lhcgr) genes were found in the testes of *A. polyacanthus* reared in +3°C relative to males reared in control temperature (Veilleux et al., 2018). These receptors are essential to bind the gonad-stimulating hormones and their reduced expression could play a role in the downturn in reproductive output. Lastly, when both sexes developed in warm water and then reproduced at control conditions, a combination of the effects observed for male and female developmental exposure alone occurred. Specifically, clutches were smaller resulting in fewer total eggs per pair, embryonic development increased, and hatchlings had larger yolks compared to pairs in control conditions. Similarly, *A. polyacanthus* pairs developing at +3°C and reproducing at control conditions produced smaller clutches, fewer total eggs, and larger yolks (Donelson et al., 2016). While larger eggs or yolks likely increase offspring growth and survival, they likely drain resources from the mother and therefore this typically results in a trade-off between offspring size/quality and the number of offspring produced (Fox et al., 1997; Lim et al., 2014). The pattern of producing two clutches of fewer but higher quality offspring, as observed when mothers and fathers were exposed to warming in development, could be an adaptive strategy when larger offspring are disproportionately selected for in certain environmental conditions (Fox et al., 1997).

Reproductive exposure to warming resulted in fewer and poorer quality offspring. Specifically, when both sexes developed at control conditions but reproduced in warmer water, pairs produced fewer clutches, embryos developed faster, and hatchling weight and standard length decreased compared to pairs that reproduced in control conditions. Similarly, reproductive and offspring characteristics were negatively impacted when anemonefish, red abalone, butterflies, and stickleback fish were exposed to elevated temperature only as adults (Fischer, Eenhoorn, et al., 2003; Fuxjäger et al., 2019; Miller et al., 2015; Vilchis et al., 2005). Reproduction in fish typically occurs within a narrow thermal window and our results suggest that an increase of +1.5°C would push summer temperature beyond the optimal window for reproduction in *A. polyacanthus*. This is consistent with an increase in exercise-related mortality at 1.5°C above average summer temperatures in a low latitude population of *A.*

polyacanthus (Rodgers et al., 2018), which suggests that *A. polyacanthus* populations already live close to their thermal optimum. Further, a shorter embryonic duration and smaller hatch size of offspring from parents that reproduced in warmer temperature are consistent with the effects of temperature on developmental and metabolic rates in fishes (Munday, Jones, Pratchett, & Williams, 2008). Since the embryos developed in the same temperature as their parents and metabolic rates are known to increase with temperature, this leads to a faster embryonic development and concomitantly smaller size at hatching.

Developmental and reproductive exposure to warming by either or both sexes generally had negative synergistic effects on reproduction and offspring. Solely male development in higher temperature led to a lower reproductive output, whereas pairs reproducing in higher temperature produced faster developing embryos and fewer and poorer quality hatchlings. When males were exposed to higher temperature in both developmental and reproductive life-stages, but females developed in control conditions, I observed the same negative effects for development and reproduction alone, but they were generally larger in magnitude, plus egg size was also impacted. Thus, prolonged exposure to higher temperature by males would likely have substantial effects on reproductive output in a future warmer ocean. However, it should be noted that although males developing and reproducing in higher temperature produced fewer and poorer quality offspring, the pairs still bred in similar proportion to control pairs. Conversely, only one breeding pair reproduced when females had prolonged exposure to warming, irrespective of the males' developmental temperature (0-3% median breeding probability), and the single clutch they produced had very high embryonic mortality. Our findings reflect previous work on *A. polyacanthus* where life-long increased temperatures for both sexes resulted in cessation of or a decline in breeding (Donelson et al., 2014, 2016), but our results suggest it is likely the effect of elevated temperature to females that is driving this response. Our results also demonstrate that female developmental exposure to warming does not necessarily allow developmental plasticity to maintain reproductive performance if warming continues past development. Similarly, female seed beetles exposed to higher temperature during development and reproduction had a lower lifetime fecundity than beetles exposed to higher temperature in only one life-stage or not at all (Stillwell & Fox, 2005). The negative effects on reproduction in our study by prolonged exposure to warming for either sex could be explained by a chronic stress response, where the focus is switched to other physiological processes for survival at the expense of reproduction. Normally, the stress axis (hypothalamic–pituitary–interrenal axis in fish) manages change through the release of glucocorticoid hormones with the aim to maintain homeostasis (Beldade, Blandin, O'Donnell,

& Mills, 2017). Prolonged stress (i.e. warming) may cause persistently elevated glucocorticoid hormones, shifting the hormone baseline such that homeostatic overload occurs (Angelier & Wingfield, 2012; Pankhurst & Munday, 2011; Romero, Dickens, & Cyr, 2009). As demonstrated by the correlation between reduced fecundity and hormonal stress responses of wild anemonefish living on bleached anemones during a marine heatwave (Beldade et al., 2017). Overall, this implies the duration of exposure to increased temperature by males and females is important to consider, and that prolonged exposure to warming will likely result in population declines as a consequence of marked reductions in reproductive output.

While family had an influence on reproduction and offspring performance, the magnitude of the effect was smaller than parental exposure to warming. This confirms that the previously discussed thermal effects are indeed due to phenotypic variation in these traits. This might suggest there is limited ability for *A. polyacanthus* to genetically adapt to warming in terms of the reproductive and offspring traits I measured. However, I only had six family lines to start the experiment and could not instigate a diallel breeding design that would enable us to estimate additive genetic effects with confidence (Munday et al., 2013). Male and female family effects in the present study's analysis are likely to reflect both genetic variance and some non-genetic effects. Nevertheless, family-level effects were comparatively minor compared with the treatment effects, suggesting that the genetic variation in the reproductive traits measured is not especially high. More generally, genetic variance in fitness related traits is predicted to be low because strong selection on such traits will erode genetic variance through time (Fisher, 1930; Mcfarlane et al., 2014; Teplitsky, Mills, Yarrall, & Merilä, 2009). Indeed, Salles et al. (2020) recently demonstrated very low genetic variance in lifetime reproductive success in a wild clownfish population. By contrast, Munday, Donelson, and Domingos (2016) have previously demonstrated there is substantial additive genetic variance in metabolic traits and growth rate in *A. polyacanthus*, including at +1.5°C. Although family-level effects on reproduction were minimal, I found females provided greater variation in breeding and clutch related traits than males, which likely reflects some component of maternal effects in addition to genetic effects. Fathers provided greater variation in hatching weight than mothers, whilst fathers and mothers contributed equally to family-level variation in the remainder of the traits.

One striking difference between this present study and previous work is the addition of daily temperature cycles. Additional investigations are required; however, it seems by incorporating a diurnal temperature cycle of ±0.6°C, which mimicked natural conditions of the collection location of the wild-caught generation, the effects of warming on reproduction and

offspring performance are accentuated. Previous findings suggest that *A. polyacanthus* from the same region of the Great Barrier Reef can restore their reproductive capacity to control levels with stable +1.5°C for one generation (Donelson et al., 2014). By contrast, I observed disrupted breeding in pairs of males and females exposed during developmental and reproductive periods to +1.5°C with a daily variation, which instead matches previous results for *A. polyacanthus* reared at a stable +3°C (Donelson et al., 2014, 2010, 2016). This could mean more dramatic effects to reproduction and offspring performance will occur in natural settings at a lower increase than stable temperature experiments suggest. This is interesting since predictable environmental variability, like diurnal temperature variation, may be expected to promote adaptive plasticity but when organisms exist near their thermal limits, as coral reef fishes often do, it's not surprising that thermal variability exacerbates effects (Kroeker et al., 2020; McLeod et al., 2014; Rummer et al., 2014). Accordingly, this highlights the importance of replicating natural conditions as much as possible in experimental settings to accurately predict climate change impacts.

The thermal history of organisms can impact reproductive output and offspring performance. This study shows that the effects of ocean warming can be sex and exposure timing specific and additionally these effects occur in synergy, additively, and opposing directions, thus making the projection for a population response to future warming highly complex. Further, it suggests that while plasticity to warming may be adaptive for some organisms (Sandoval-Castillo et al., 2020), it is not for others. This study also stresses the importance of producing the most relevant simulations of environmental change feasible in the laboratory, as aspects like natural diurnal cycles may influence phenotypic effects. This study highlights the importance of considering life-stage and sex-specific exposures to warming to accurately predict how populations and species may cope with climate change.

Chapter 4 Parents Exposed to Warming Produce Offspring Lower in Weight and Condition

4.1 Abstract

The parental environment can alter offspring phenotypes via the transfer of non-genetic information (parental effects), and can be viewed as an extension of (within-generation) phenotypic plasticity. Smaller size, poorer physical condition and skewed sex ratios are common responses of organisms to global warming, yet whether parental effects may alleviate, exacerbate, or have no effect on these has been underexplored. Further, the relative non-genetic influence of mothers and fathers and ontogenetic timing of parental exposure on offspring phenotypes is poorly understood. Here, I tested how maternal, paternal, and biparental exposure of a coral reef fish to elevated temperature (+1.5°C) at different ontogenetic stages (development vs reproduction) influences offspring length, weight, body condition and sex ratios. The spiny chromis damselfish (*Acanthochromis polyacanthus*) was reared across two generations in present-day and projected ocean warming in a full factorial design. As expected, offspring of parents exposed to present-day control temperature that were reared in warmer water were shorter than their siblings reared in control temperature; however, within-generation plasticity allowed maintenance of weight, resulting in a higher body condition. Parental exposure to warming, irrespective of ontogenetic timing and sex, resulted in lighter and lower condition offspring in all rearing temperatures. Combined with previous studies, reduced weight might be the result of a negative genetic correlation with an adaptive parental effect, such that warm-exposed parents produce offspring that maintain metabolic rate in ambient elevated temperatures but at a cost of reduced weight and subsequent loss of body condition. By contrast, offspring sex ratios were not strongly influenced by their rearing temperature or that of their parents. Together, my results reveal that within-generation plasticity and parental effects can result in trade-offs between traits and/or costs. Within-generation plasticity may help coral reef fishes maintain or even improve performance in a warm ocean. Parental effects, however, appear to exacerbate the negative effects of warming, which could hasten the decline of populations in a warm future ocean. Alternatively, the impact on offspring morphology may be a necessary cost to adapt metabolism to increasing temperatures. Nevertheless, parental effects can clearly be influential regardless of when mothers and fathers are exposed to warming. This research highlights the importance of examining phenotypic plasticity within and between generations across a range of traits to accurately predict how organisms will respond to climate change.

4.2 Introduction

Rapid environmental change poses a threat to biological systems through effects on the phenotypic traits of individual organisms that influence population sustainability. Smaller body size, reduced physical condition and skewed sex ratios are common responses of ectotherms to global warming (Geffroy & Wedekind, 2020; Reading, 2007; Sheridan & Bickford, 2011). Reduced size and condition at higher temperatures are often due to increased metabolic rates alongside an inability to compensate with greater food intake or reallocate energy (Sheridan & Bickford, 2011). For marine fishes, a 20% reduction in assemblage-averaged maximum body weight has been predicted by 2050 owing to warming, which has ramifications for ecosystem productivity and fisheries harvest potential (Cheung et al., 2013). Shrinking body length and weight with decreasing latitude is one of the most widely observed patterns in nature, suggesting a reduced body size may be adaptive owing to increased thermal tolerance or early maturation (Angilletta Jr, Steury, & Sears, 2004; Forster et al., 2012; Leiva, Calosi, & Verberk, 2019; Verberk et al., 2020). However, reduced body size and condition can increase predation risk, reduce fecundity, and decrease competitive ability (Blueweiss et al., 1978; Booth & Hixon, 1999; Goatley & Bellwood, 2016; Grorud-Colvert & Sponaugle, 2006; Meekan et al., 2006; Poulos & McCormick, 2015). Sex ratios are also an important component of population sustainability since reproduction typically depends on the availability of males and females. Increased temperatures can bias sex ratios in reptiles, and to a lesser extent amphibians and fishes, owing to temperature-dependent sex determination during early development (Bickford, Howard, Ng, & Sheridan, 2010). Population growth is often constrained by female fecundity (Hill, Lycett, & Dunbar, 2000; Morales, Bretagnolle, & Arroyo, 2005), so in species where increased temperatures lead to a male bias, like fishes (Geffroy & Wedekind, 2020), warming can pose a threat to population replenishment. Yet, organisms may be able to maintain body length, weight, condition or sex ratios in a future warm world through phenotypic plasticity (non-genetic response to environmental variation; Pigliucci, 2001)(Donelson & Munday, 2015; Salinas & Munch, 2012; Shama, 2015). Plasticity is predicted to be especially important in responding to rapid climate change because it typically operates over a much faster timescale than adaptation by natural selection (Geoghegan & Spencer, 2012; Klironomos et al., 2013).

The environment may induce phenotypic change both within a single generation (within-generation plasticity) and across generations (parental effects). Parental effects occur through the transfer of non-genetic information via epigenetics (e.g. DNA methylation, histone modification, or small non-coding RNAs), cell structures, hormones, nutrients, or behaviours (Bonduriansky et al., 2012; Ho & Burggren, 2010). Parents may anticipate offspring conditions

in order to produce progeny with the best phenotype for that environment (Donelson & Munday, 2015; Marshall & Uller, 2007; Shama & Wegner, 2014). Defined as anticipatory parental effects, they are considered adaptive when offspring performance improves in the environment that is predicted by the parental environment, but may be maladaptive when offspring conditions differ from those experienced by parents (Burgess & Marshall, 2014). The risk of a mismatch between the anticipated and actual environment will tend to select against anticipatory parental effects and may explain the weak evidence across taxa (Bonduriansky & Crean, 2018; Radersma et al., 2018; Sánchez-Tójar et al., 2020; Uller et al., 2013). By contrast, carry-over parental effects – where the parental environment influences offspring phenotype regardless of the offspring environment – are likely widespread because they are not contingent on environmental predictability and therefore don't require complex machinery to assess environmental conditions and adjust offspring phenotypes accordingly (Bonduriansky & Crean, 2018; Jablonka et al., 1995). While carry-over parental effects can be adaptive, since the transfer of a high parental condition to offspring would be beneficial in many circumstances (Bonduriansky & Crean, 2018; Jablonka et al., 1995), they may also be maladaptive (Evans, Lymbery, Wiid, Rahman, & Gasparini, 2017; Marshall & Uller, 2007; Valdivieso et al., 2020) when a low parental condition is passed on (but see positive net selection argument in Bonduriansky & Crean, 2018). Therefore, in order to predict the effect of future warming on ectotherms it is necessary to understand whether plasticity within and between generations may be beneficial or exacerbate the negative effects of warming.

Parental effects may derive from mothers, fathers or both parents. Maternal effects are generally assumed to be more important than paternal effects owing to the mother's role in embryonic nutritional provisioning and the transfer of mitochondria (Ghiselli & Milani, 2020; Mousseau & Fox, 1998). However, this classic idea is a simplistic view of maternal and paternal contributions, with both parents often having a genetic (i.e. DNA) and non-genetic (e.g. epigenetic) influence on offspring phenotypes (Bonduriansky & Day, 2009). Furthermore, paternal provisioning (e.g. nuptial gifts or substances for embryos) and care may increase selection for paternal effects (Griffith, Owens, & Burke, 1999; Hunt & Simmons, 2000; Smedley & Eisner, 1996). Maternal or paternal effects may evolve under sex-specific patterns in reproductive strategies, socialising, foraging, predation, or parasitism (Burke et al., 2020; Lewis et al., 2002; Magnhagen, 1991; Ruckstuhl, 2007; Zuk & McKean, 1996). But even when the sexes are alike, it is possible that mothers and fathers experience different environments when temporal environmental variation exists and breeding pairs are of mixed age (Mills, 1973) or

large spatial areas are traversed (Shimada et al., 2020); therefore, leading to the potential for differing maternal and paternal effects.

Whether maternal and/or paternal effects occur may also depend on the ontogenetic timing of parental exposure, with early periods in development most sensitive to environmental change (West-Eberhard, 2003). For example, developmental exposure to stressful conditions, such as a heatwave, can allow individuals to cope better with those same conditions later in life and this benefit may be passed to offspring (Donelson, Munday, McCormick, et al., 2012). By contrast, parents that reproduce during stressful conditions may have insufficient resources for their offspring, resulting in negative parental effects (Donelson et al., 2016; Fuxjäger et al., 2019; Radersma et al., 2018). Currently, great interest exists for plasticity research in a climate change context (Donelson et al., 2018; Gunderson & Stillman, 2015; Reusch, 2014; Seebacher et al., 2015); however, owing partly to the logistical challenges, I am not aware of a study that has explored the ontogenetic timing of maternal and paternal effects and their interaction with offspring environments in a tropical ectotherm. Examining both timing and sex-specific parental effects will provide a greater understanding of plasticity across generations and enhance our capacity to predict if and how plasticity within and between generations may help tropical ectotherms cope with warming.

Here, I investigated the ontogenetic timing of paternal, maternal, and biparental exposure to elevated temperature on offspring size, condition, and sex ratios in a coral reef damselfish, *Acanthochromis polyacanthus* (Bleeker 1855). Specifically, males and females developed from hatching in a present-day average temperature for their population (control), or 1.5°C above the average temperature, consistent with climate change projections and heatwaves that already occur in marine ecosystems (Frölicher et al., 2018; IPCC, 2019). Once mature (1.5 years), the fish were divided orthogonally into control and elevated reproductive temperatures and breeding pairs were created such that every thermal combination of sex and time (development, reproduction, or both) occurred (eight parental treatments). Offspring from these breeding pairs were reared at the present-day average summer temperature (control), +0.75°C and +1.5°C for three months, at which time offspring standard length, weight, Fulton's K condition factor, and sex ratios were measured. Six families were used to start the experiment. This experimental design allows estimation of the relative non-genetic maternal and paternal contributions, parental timing effects, within-generation plasticity and family-level (i.e. mostly genetic) effects. I hypothesised that anticipatory parental effects were common because the parental environment could be predictive of the offspring environment owing to

their life-history (although carry-over parental effects may also be common for the reasons previously mentioned). Furthermore, the fact this species is morphologically identical and monogamous with biparental care implies both paternal and maternal effects may be favoured. I further hypothesised offspring may benefit more from parental exposure to warming in development rather than reproduction because *A. polyacanthus* adults appear to have limited capacity for plasticity compared to juveniles (Chapter 2; Chapter 3; Donelson & Munday, 2015; Donelson, Munday, McCormick, & Nilsson, 2011; Donelson et al., 2010; Rodgers, Donelson, McCormick, & Munday, 2018).

4.3 Methods

4.3.1 Study species

A. polyacanthus is common on coral reefs in the Indo-Australian archipelago (Robertson, 1973). They form monogamous pairs and breed primarily during summer (Robertson, 1973; Thresher, 1985). Egg clutches are laid in caves with biparental care occurring during embryogenesis and several weeks post hatching (Kavanagh, 2000; Robertson, 1973; Thresher, 1985). Consequently, these potentially sensitive life-stages are likely already experiencing high temperatures during summer marine heatwaves (Chapter 2; Dahlke et al., 2020; Frölicher et al., 2018). Since *A. polyacanthus* lack a dispersal larval stage and adults are site attached with small home ranges (Miller-Sims et al., 2008; Robertson, 1973), they are unlikely to migrate to more favourable environments under climate warming. This includes moving to deeper waters, which anyway would provide little relief within their depth range (i.e. the thermocline is typically much deeper; Frade et al., 2018; Jankowski et al., 2015; Lieske & Myers, 1994; Walther et al., 2013). *A. polyacanthus* was chosen as a model because acute elevated temperature has been shown to strongly affect individual performance (Donelson et al., 2010; Munday, Kingsford, et al., 2008; Rummer et al., 2014), but biparental effects can partially or fully mitigate the negative impacts of elevated temperature on offspring (Donelson & Munday, 2015; Donelson, Munday, McCormick, et al., 2012; Donelson et al., 2016). The life history, reproductive strategy and tight fidelity of *A. polyacanthus* means temporal environmental variation is most likely to explain differing maternal and paternal developmental thermal histories in natural populations, for example in mixed age pairs one parent may have developed during a marine heatwave and the other during a year of usual sea temperature, or differing developmental and/or reproductive temperatures between pairs.

4.3.2 Experimental design

Two generations of *A. polyacanthus* were reared in environmentally controlled conditions to examine temperature-induced parental effects. A detailed description of the F0 and F1 generations and the aquaria facility are provided in Chapter 3. Briefly, the experiment began with six wild-caught pairs from the Palm Islands region (18° 37′ S, 146° 30′ E) of the central Great Barrier Reef to account for genotypic variation (F0 generation, figure 4.1). Pairs were kept at seasonally cycling present-day temperature based on the Palm Islands region and were provided half a terracotta pot as a spawning site. The F0 generation bred in the Austral summer of 2016. Egg clutches were kept with the parents until hatching, allowing them to provide nest care as occurs in the wild. Newly hatched F1 generation siblings were divided between a present-day control and +1.5°C temperature treatment, with 10 fish per tank and a minimum of five replicate tanks per clutch (figure 4.1). A 1.5°C increase already occurs on the Great Barrier Reef during marine heatwaves (Chapter 2; Frölicher et al., 2018; Hughes et al., 2019) and is projected to occur as an average temperature by 2050 – 2100 (IPCC, 2013). The control water temperature simulated seasonal (winter minimum 23.2°C, summer maximum 28.5°C) and diurnal (0300hrs -0.6°C, 1500hrs +0.6°C) cycles for the Palm Islands region based on temperature loggers from 2002 to 2015 at 0.2-14.6m depth (AIMS, 2016), with the elevated treatment matching this but 1.5°C higher. Similarly, the photoperiod of the Palm Islands region was replicated, reaching a maximum of 13h 15min light in summer (December) and a minimum of 11h 01min light in winter (June). Seasonal changes to water temperature and illumination were adjusted weekly.

In the Austral winter of 2017, the F1 generation reached maturity and were paired for breeding so that: 1) both males and females developed in control (♂♀), 2) only males developed in +1.5°C (♂♀), 3) only females developed in +1.5°C (♂♀), or 4) both males and females developed in +1.5°C (♂♀). These four pair combinations were further divided into present-day control (♂♀) and +1.5°C (♂♀) reproductive temperatures, which resulted in eight parental temperature treatments (♂♀, ♂♀, ♂♀, ♂♀, ♂♀, ♂♀, ♂♀, ♂♀; figure 4.1). I crossed males and females of one family with another following figure 1A in Bonduriansky, Crean, and Day (2012) such that I had three family crosses from the original six F0 families. Once breeding pairs were successfully established (see Chapter 3), the number of replicate pairs per parental treatment inclusive of families was 19 (♂♀), 17 (♂♀), 17 (♂♀), 10 (♂♀), 19 (♂♀), 17 (♂♀), 11 (♂♀), 13 (♂♀). In the Austral summer of 2017/2018, the F1 generation bred, although no reproduction occurred when both males and females developed and reproduced in +1.5°C (♂♀) and only one clutch was produced when males developed in control, females developed in +1.5°C, and reproduction was in +1.5°C (♂♀; Chapter 3). This

one clutch experienced exceptionally high embryonic mortality (74%) and the uncertainty in estimates from the few offspring that hatched meant this treatment was excluded from analyses (Chapter 3). Owing to logistics but also following what occurs in the wild, egg clutches were kept with the parents until hatching. However, this means for offspring of parents exposed to an elevated reproductive temperature (♂♀🔥 and ♂♀🔥), I cannot disentangle the effects of parental reproductive temperature versus early developmental plasticity. It is important to note that the hatching data presented in Chapter 3 was from all first clutches produced during the entire summer breeding season, whereas the current chapter presents a subset of the clutches that were reared post hatching (though results are almost identical).

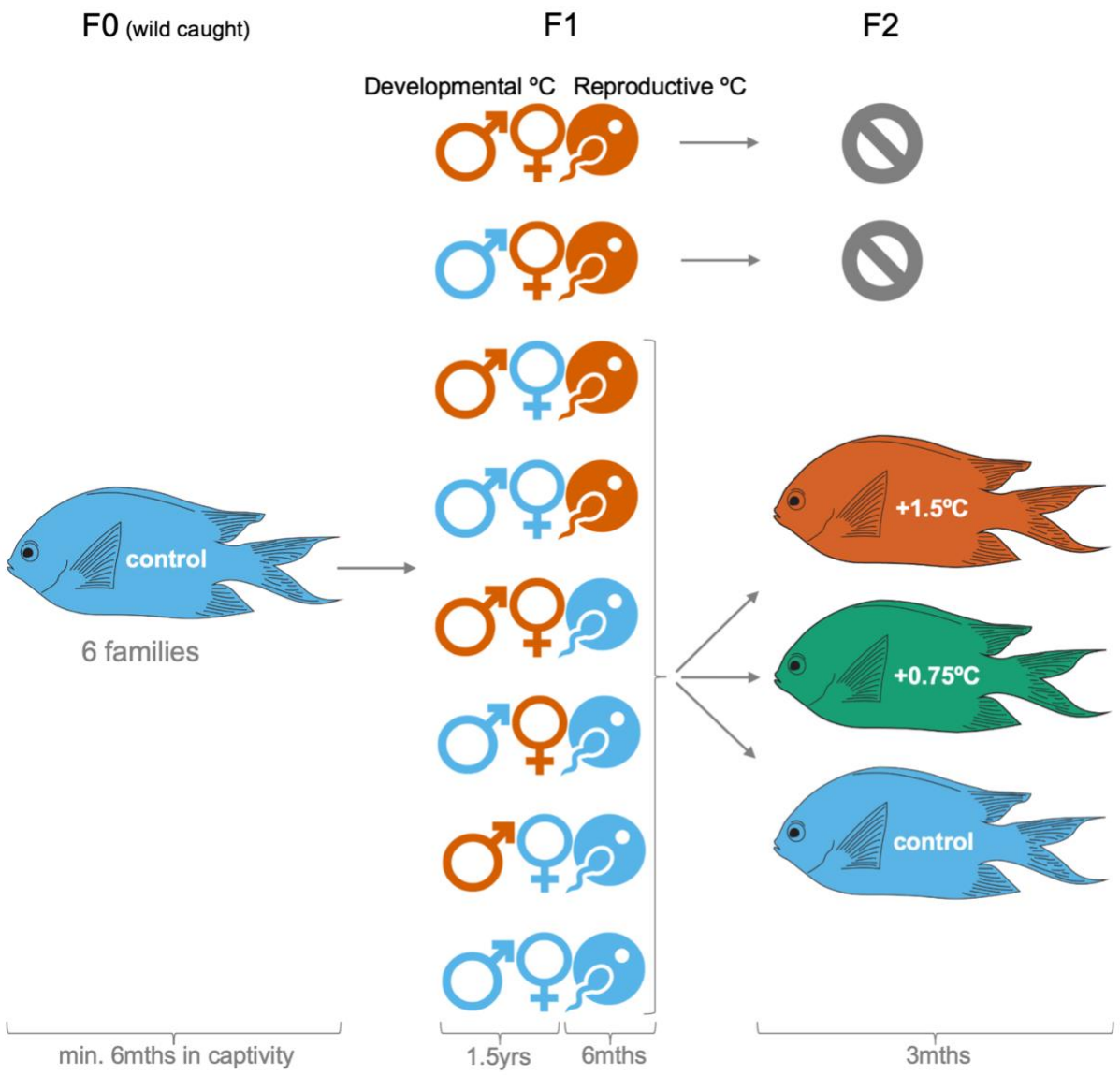

Figure 4.1 Experimental design. Newly hatched A. polyacanthus from six wild-caught families (F0) were split between two developmental temperatures; a present-day average temperature for their population (control – blue sex symbols) and 1.5°C above the average temperature (orange sex symbols). At maturity F1 fish were further divided into present-day control (blue egg and sperm) and +1.5°C reproductive temperatures (orange egg and sperm). Breeding pairs were created of reciprocal sex crosses of the developmental temperatures across both reproductive temperatures, which resulted in eight F1 parental treatments. ⃠ *indicates the two F1 treatments that did not reproduce. Newly hatched siblings (F2) were split among a present-day average summer temperature of 28.5°C (control), 29.25°C (+0.75°C), and 30°C (+1.5°C). Please note that for logistical reasons offspring were kept with their parents until hatching, i.e. embryos were exposed to the parent's reproductive temperature.*

Newly hatched F2 generation siblings were split among a present-day average summer temperature of 28.5°C (control), 29.25°C (+0.75°C), or 30°C (+1.5°C; figure 4.1). Each temperature treatment had a daily temperature cycle of –0.6°C at 03:00 hours and +0.6°C at 15:00 hours matching the natural diurnal temperature variation experienced by this population in the wild (AIMS, 2016). For each clutch, siblings were stocked at a density of approximately 20 fish per tank over two replicate tanks for each temperature treatment. A total of 31 clutches were reared to approximately three months of age. I incorporated +0.75°C rearing temperature as it is a half-way point between potentially favourable and unfavourable thermal environments. This F2 rearing treatment that was intermediate to the parental control and +1.5°C temperatures allowed me to observe if 1) any temperature shift (i.e. an increase or decrease) between generations induced phenotypic change and 2) a smaller temperature increase within and between generations is more beneficial than a larger temperature increase (Donelson et al., 2016). Lastly, by manipulating both parent and offspring environments across a range of ecologically relevant temperatures I could detect within-generation plasticity and different types of parental effects (Bonduriansky & Crean, 2018; Donelson et al., 2018).

Hatchlings were given 2–3 hours to slowly equilibrate to their rearing temperature via a 2 L tub floated in the tank and receiving gradual inflow. Hatchlings were fed live *Artemia nauplii* the first 6 days (approximately 417 mg dried artemia cysts per tank). On day 4, they began 200–400µm NRD pellets (INVE Aquaculture Salt Lake City, UT, USA) supplied daily at 40 mg $tank^{-1}$. Between days 30 to 59 they were fed 500–800µm NRD pellets supplied daily at 202 mg $tank^{-1}$ and then on day 60 increased to 404 mg $tank^{-1}$. This is considered a high feeding level (approximately 2% of their body weight at 3 months post hatching) for captive *A. polyacanthus* on an energy-rich formulated diet (Donelson et al., 2010). During rearing there was approximately 9% natural mortality of juveniles (appendix figure 4.1). There was also mortality from two incidents of equipment failure (~3% of juveniles); one caused an ammonia spike (~0.25 ppm), the other oxygen supersaturation, but deaths were evenly spread across treatments and surviving fish did not appear stressed. The F2 generation were maintained in a 15,000 L recirculating system supplied with a continuous flow of natural seawater with precise temperature control (smaller replica of F0 and F1 generations' aquaria facility described in Chapter 3).

4.3.3 Size and sex ratios

Within hours of hatching, approximately 20 offspring (F2 generation) from each clutch to be reared were euthanised by an overdose of clove oil, weighed (±0.1 mg; excess water removed with a Kimwipe) and photographed. Hatch standard length (±0.01 mm) and yolk area (±0.01 mm^2) were determined from the photographs, by one person (B. Spady) who was blinded to the treatments, using ImageJ software v. 1.50i (Schneider, Rasband, & Eliceiri, 2012). A total of 596 hatchlings were measured. The standard length of 4 hatchlings and the yolk area of 7 hatchlings could not be accurately determined and therefore were not included.

As described above from each clutch two replicate tanks of 20 siblings per F2 treatment were grown until approximately three months of age. A total of 3419 juveniles were sexed in a water-filled clear bag under the microscope via external examination of the urogenital papilla by two experienced researchers (R.K. Spinks or J.M. Donelson; Hilder & Pankhurst, 2003; Robertson, 1973). The juveniles were then euthanised by cervical dislocation, weighed (±1 mg), and standard length measured (±0.02 mm). The sex of 31 juveniles, weight of 4 juveniles, and standard length of 6 juveniles could not be accurately determined and were therefore excluded. Offspring were sexed and measured specifically between 79-106 dph (mean 95 dph) due to molecular sampling and swimming performance tests performed in a subset of these fish over this period of time but not presented here. Fulton's K condition factor was calculated as:

$$K = 100\frac{W}{L^3}$$

Whereby W is wet weight, L is standard length, and the scaling factor is used to bring the condition closer to one (Froese, 2006; Ricker, 1975). Fulton's K condition factor is a widely used proxy for body condition in fishes, nevertheless, it has been criticised (Froese, 2006; Jones, Petrell, & Pauly, 1999; Nash, Valencia, & Geffen, 2006). A common alternative is to model weight as a function of length, however, during preliminary analysis I found that the results were identical to Fulton's K condition factor.

4.3.4 Statistical analysis

Bayesian mixed models were applied using the rstanarm package v. 2.21.1 (Goodrich et al., 2020) in R v. 4.0.3 (R Core Team, 2020). The standard length, weight, or yolk area of newly hatched offspring were dependent variables and modelled with normal distributions (e.g. LMMs). Models were validated visually and followed linear model assumptions of linearity, homogeneity of variances, and normality. Each model included F1 temperature ( ,  ,  ,  ,

♂♀, ♂♀) as an independent fixed variable. Each model's random intercept varied by father family (6 levels) and mother family (6 levels) due to non-independence between offspring from the same F0 family line of the father and between offspring from the same F0 family line of the mother. The random intercept also varied by F1 pair (30 levels) due to non-independence between offspring from the same parent. Random slopes in addition to random intercepts did not improve the model fits visually or based on Bayesian leave-one-out cross-validation (LOO Vehtari, Gelman, & Gabry, 2017)

Offspring standard length, weight, or Fulton's K condition factor at approximately three months of age were dependent variables and modelled with gamma distributions and log links (e.g. GLMMs). These were better fits visually than with normal distributions where assumptions of normality were not met and heteroscedasticity was evident in the weight model. Though using a Gamma distribution meant that r^2 could not be accurately estimated. Each model included the independent fixed variables F1 temperature (♂♀, ♂♀, ♂♀, ♂♀, ♂♀, ♂♀), F2 temperature (28.5°C, 29.25°C, 30°C), their interactions, and the covariates of offspring age and density (centered and scaled). These covariates were included because offspring were measured between 79-106 dph (mean 95 dph) and fish density varied between 4-31 fish (mean 20) per tank owing to small clutches, deaths, or miscounting. The range of ages and densities overlapped in the F1 and F2 temperature treatments and there was no evidence of significant interactions between them. Finally, sex ratio was a dependent variable and modelled with a Binomial distribution and log odds link (e.g. GLMM). The model was validated visually. The independent fixed variables were F1 temperature (♂♀, ♂♀, ♂♀, ♂♀, ♂♀, ♂♀), F2 temperature (28.5°C, 29.25°C, 30°C), and their interactions.

Offspring standard length, weight, Fulton's K condition factor, and sex ratio models at three months had the same random effects structure owing to the hierarchical nature of the experimental design and to prevent pseudoreplication. Each model's random intercept varied by father family (6 levels) and mother family (6 levels) due to non-independence between offspring from the same F0 family line of the father and between offspring from the same F0 family line of the mother. The random intercept also varied by F2 rearing tank (181 levels) nested in F1 pair (30 levels) due to non-independence between offspring from the same tank and offspring from the same parent. Random slopes in addition to random intercepts did not improve the model fits visually or based on LOO. Variation attributed to random effects are stated in the link scale.

Bayesian models allow integration of prior knowledge (van de Schoot et al., 2021). I specified weakly informative priors using rstanarm (appendix table 4.1). The posterior distribution is derived from the priors (previous evidence) and the likelihood function (new evidence; van de Schoot et al., 2021). Visual posterior checks confirmed that priors never heavily influenced the posterior. Using the Hamiltonian Monte Carlo algorithm, models were run with three chains by means of the No-U-Turn sampler for a minimum 5000 iterations with at least every second posterior sample thinned and a minimum of 40% discarded depending upon the complexity of the model. Bayesian model validation followed Chapter 2. In order to compare among parental temperatures without confounding offspring rearing temperature effects, groups were compared to their respective offspring rearing temperature (28.5°C, 29.25°C, or 30°C) of control parents (♂♀). Statistical significance is determined by probability, which is calculated from the posterior distribution. Probabilities are displayed as a percent on figures and in tables. The closer a probability is to either 100% or 0% suggests greater confidence in a group being smaller/larger relative to its comparison, whereas nearer to 50% suggests little confidence in a group being smaller/larger relative to its comparison. Note that Bayesian inference (with suitable priors) doesn't require correction for multiple comparisons (Gelman & Tuerlinckx, 2000). Figures were created with the R packages' emmeans v. 1.5.1 (Lenth, 2020) and tidybayes v. 2.1.1 (Kay, 2020).

4.4 Results

4.4.1 Maternal exposure to warming produced hatchlings with larger yolks while reproductive exposure decreased hatchling length and weight

Parental reproductive temperature had a greater overall effect on newly hatched offspring length and weight than did parental developmental temperature (figure 4.2A, B). By contrast, maternal developmental temperature affected newly hatched offspring yolk reserves (figure 4.2C). Hatchlings of control parents (♂♀) were a median 5.17 mm standard length and 3.31 mg weight with 1.47 mm^2 yolk area. Hatchlings of parents where the father, mother, or both parents developed in +1.5°C, but reproduced in control temperatures (♂♀, ♂♀, or ♂♀), were similar in length and weight compared to hatchlings of control parents (♂♀; figure 4.2A, B). When mothers developed in +1.5°C (♂♀ and ♂♀), hatchlings had a median 14% and 18% larger yolk areas than progeny from control parents (♂♀; figure 4.2C). When both parents developed in control temperatures, but reproduced in +1.5°C (♂♀), their hatchlings were a median 4% shorter compared to hatchlings of control parents (♂♀; figure 4.2A), but they

were similar in weight (figure 4.2B). When fathers developed in +1.5°C, mothers developed in control temperature, and reproduction was in +1.5°C (♂♀) they produced hatchlings similar in length compared to hatchlings of control parents (♂♀; figure 4.2A) and to pairs where the father developed in +1.5°C, but reproduced in control temperature (♂♀). However, these hatchlings (♂♀) were a median 16% lighter compared to hatchlings of control parents (♂♀ ; figure 4.2B) and a median 17% lighter compared to hatchlings of fathers that developed in +1.5°C and reproduced in control conditions (♂♀; 96% probability of weighing less).

Variation attributed to paternal and maternal family-level effects were less than the magnitude of parental temperature effects (standard length σ 0.02 mm, weight σ 0.03 mg, yolk area σ 0.01 mm^2). Variation attributed to F1 pair was equivalent to or lower than family-level effects for standard length and yolk area but slightly higher for weight (σ 0.1 mg).

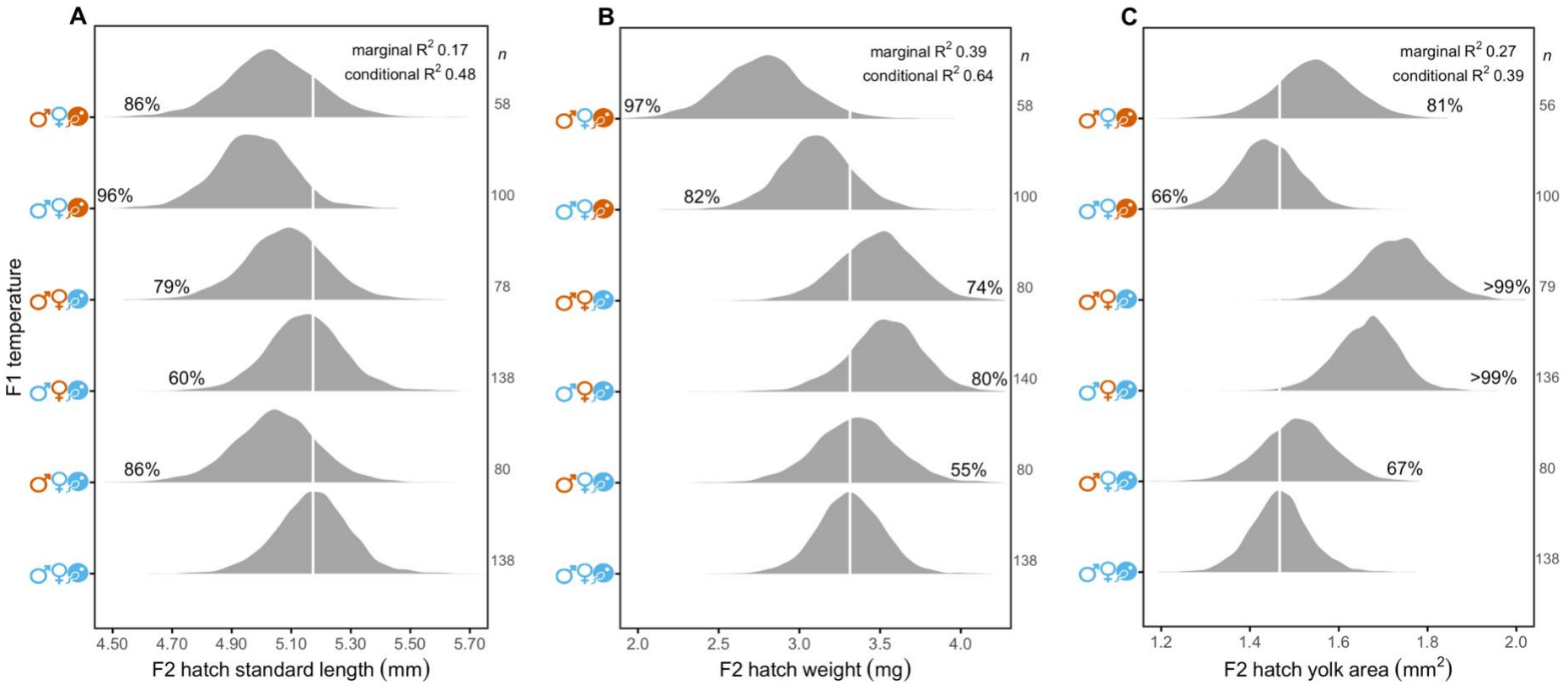

Figure 4.2 Hatchling size and yolk area. Bayesian posterior density distributions of offspring A) standard length, B) weight, and C) yolk area at hatching from each parental temperature (♂♀, ♂♀, ♂♀, ♂♀, ♂♀, ♂♀). The father and mother's developmental temperature is represented by sex symbols and the reproductive temperature by an egg and sperm icon whereby blue denotes present-day control temperature and orange a temperature increase of 1.5°C. Posterior probabilities (i.e. confidence) are expressed as a percent and shown to the left of the vertical white line when smaller in size or to the right of the line when larger in size relative to hatchlings of control parents (♂♀). Sample size (n) is number of hatchlings.

4.4.2 Offspring reared in warmer water were shorter and in higher condition

When parents developed and reproduced in control temperature (♂♀) and their offspring were reared in warmer water, juveniles were shorter, but the same weight and thus in higher condition (figure 4.3). At the average age (95 dph) and density (20 fish), offspring of control parents (♂♀) reared in 28.5°C were a median 30.70 mm standard length, 1200 mg weight, and 4.10 Fulton's K condition factor. When sibling offspring instead developed in 29.25°C or 30°C they were a median 1% or 2% shorter, respectively, compared to offspring reared in 28.5°C (♂♀; figure 4.3A). Since weight did not differ for offspring of control parents (♂♀) reared in all temperatures (28.5°C, 29.25°C or 30°C; figure 4.3B), it was not surprising that offspring that developed in 29.25°C or 30°C were in higher condition by a median of 2% or 4%, respectively, relative to offspring reared in 28.5°C (figure 4.3C).

4.4.3 Parental exposure to warming decreased offspring weight and condition

The father's developmental temperature affected offspring length, weight and condition. Offspring reared in 28.5°C from fathers developed in +1.5°C, mothers developed in control, and reproduction in control temperature (♂♀) were a median 3% shorter, 11% lighter, and 3% lower in condition compared to offspring reared in 28.5°C of control parents (♂♀; figure 4.3A, B, C). Sibling offspring reared in 29.25°C were a median 2% shorter, although there was less certainty in this trend, 8% lighter, and 4% lower in condition compared to offspring reared in 29.25°C from control parents (♂♀; figure 4.3A, B, C). When reared in 30°C, sibling offspring were a median 2% shorter, 10% lighter, and 4% lower in condition compared to offspring reared in 30°C of control parents (♂♀; figure 4.3A, B, C).

The mother's developmental temperature affected offspring weight and condition, but the effects were less marked than for the father's developmental temperature alone (above). Offspring from fathers developed in control, mothers developed in +1.5°C, and reproduction in control temperature (♂♀) were similar in length across their rearing temperatures compared to offspring of control parents (♂♀) in those same rearing temperatures (figure 4.3A). Offspring reared in 28.5°C were similar in weight and condition relative to offspring reared in 28.5°C of control parents (♂♀; figure 4.3B, C). However, there was a trend of sibling offspring reared in 29.95°C or 30°C weighing a median 3% or 7% less, respectively, compared to offspring of control parents (♂♀) in those same offspring developmental temperatures (figure 4.3B). Further, an interaction was present between mother and offspring temperatures, with offspring

reared in 29.95°C or 30°C a median 3% or 4% lower in condition, respectively, compared to offspring of control parents (♂♀) in those same rearing temperatures (figure 4.3C).

Both parent's developmental temperature affected offspring weight and condition. Offspring from fathers and mothers that developed in +1.5°C, but reproduced in control temperature (♂♀), were similar in length when reared in 28.5°C and 30°C compared to offspring of control parents (♂♀) in those same rearing temperatures (figure 4.3A). However, offspring reared in 28.5°C were a median 11% lighter and 8% lower in condition compared to offspring reared in 28.5°C of control parents (♂♀; figure 4.3B, C). Sibling offspring reared in 29.95°C tended to be lighter by a median 3%, which resulted in a median 7% lower condition compared to offspring reared in 29.95°C of control parents (♂♀; figure 4.3A, B, C). Sibling offspring reared in 30°C were a median 7% lighter and 10% lower in condition compared to offspring reared in 30°C of control parents (♂♀; figure 4.3B, C).

The parent's reproductive temperature affected offspring length, weight and condition. Offspring reared in 28.5°C from fathers and mothers that developed in control temperature but with reproduction in +1.5°C (♂♀), were a median 2% shorter, 7% lighter, and 3% lower in condition compared to offspring reared in 28.5°C of control parents (♂♀; figure 4.3A, B, C). When sibling offspring were instead reared in 29.95°C their standard length was similar, but they were a median 7% lighter and 4% lower in condition compared to offspring reared in 29.25°C of control parents (♂♀; figure 4.3A, B, C). Sibling offspring reared in 30°C were of similar length, but they were a median 6% lighter and 4% lower in condition compared to offspring reared in 30°C of control parents (♂♀; figure 4.3A, B, C).

The father's developmental and reproductive temperature affected offspring weight and condition. Offspring from fathers developed in +1.5°C, mothers developed in control, and with reproduction in +1.5°C (♂♀) were similar in length, irrespective of their rearing temperature, compared to offspring of control parents (♂♀) in those same rearing temperatures (figure 4.3A). Offspring reared in all temperatures (28.5°C, 29.95°C, and 30°C) were a median 8% lighter and 7% lower in condition compared to offspring of control parents (♂♀) in those respective rearing temperatures (figure 4.3B, C).

Comparing offspring from pairs with fathers developing in +1.5°C and mothers developing in control, and with reproduction either in control (♂♀) or +1.5°C temperatures (♂♀), showed little difference in offspring weight (probabilities ≤74%). However, offspring reared in 28.5°C and 30°C from fathers continuously exposed to +1.5°C (♂♀) were a median 2% longer compared to offspring where fathers were only exposed to +1.5°C in development (

; both 93% probability of longer length). Accordingly, this resulted in trends of lower condition by a median 3% for offspring reared at 28.5°C and 30°C compared to offspring of parents reproducing in control ( ) reared at those temperatures (87 and 85% probability of lower condition). Offspring from fathers continuously exposed to +1.5°C ( ) reared in 29.95°C were similar length and condition to offspring reared in 29.25°C of parents reproducing in control temperature (; probabilities ≤83%).

Comparing offspring from pairs with both parents developing in control temperature and with reproduction in +1.5°C ( ) or with fathers developing in +1.5°C ( ) showed little difference in offspring length or weight (probabilities ≤81%). However, offspring reared in all temperatures (28.5°C, 29.95°C, and 30°C) from fathers continuously exposed to +1.5°C showed trends of lower condition by a median 3-4% compared to offspring with fathers developing in control ( ) in the respective rearing temperatures (86-89% probability of lower condition).

Offspring standard length, weight, and Fulton's K condition factor decreased as fish density increased (appendix figure 4.2A, C, E) and offspring standard length, weight, and Fulton's K condition factor increased as fish aged (appendix figure 4.2B, D, F). Variation attributed to paternal and maternal family-level effects were less than the magnitude of parental and offspring temperature effects for standard length (σ 0.0002 log vs largest treatment effect -0.03 log), weight (σ 0.002 log vs largest treatment effect -0.1 log), and Fulton's K condition factor (σ 0.0003 log vs largest treatment effect -0.08 log). Variation attributed to F1 pair and F2 rearing tank were equivalent to or lower than family effects.

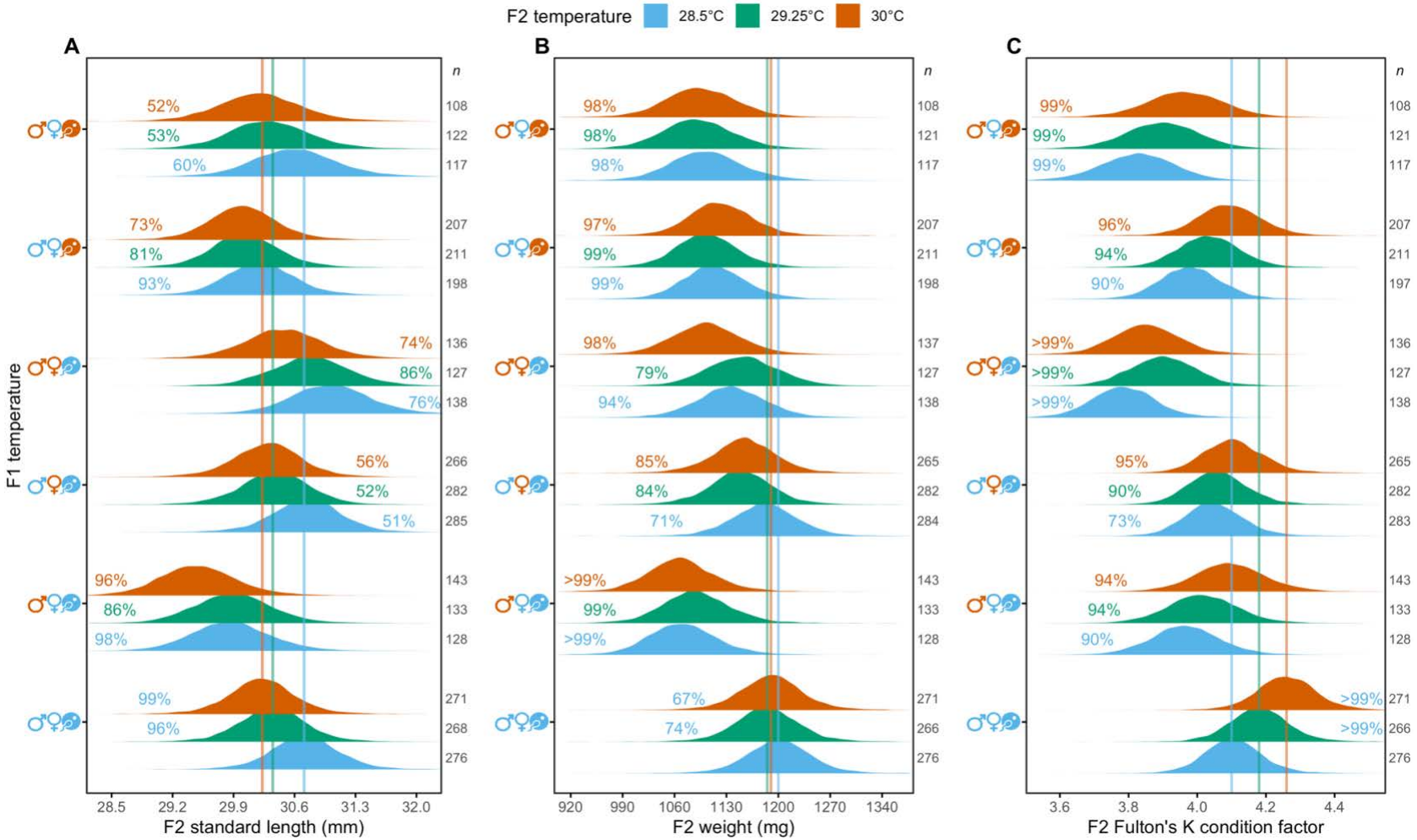

Figure 4.3 Offspring size and condition. Bayesian posterior density distributions of offspring A) standard length, B) weight, and C) Fulton's K condition factor at the average age of 95 days post hatching and density of 20 fish per tank for each parental (♂♀, ♂♀, ♂♀, ♂♀, ♂♀, ♂♀) and offspring (28.5°C, 29.25°C, 30°C) temperature. Father and mother developmental temperature is represented by sex symbols and the reproductive

temperature by an egg and sperm icon whereby blue denotes present-day control temperature and orange a temperature increase of 1.5°C. Posterior probabilities (i.e. confidence) are expressed as a percent and coloured blue when compared to offspring reared in 28.5°C (vertical blue line) of control parents (♂♀), green when compared to offspring reared in 29.25°C (vertical green line) of control parents (♂♀), or orange when compared to offspring reared in 30°C (vertical orange line) of control parents (♂♀). Probabilities to the left of the vertical lines indicate smaller size/condition relative to the comparison, whereas probabilities to the right of the vertical lines indicate larger size/condition relative to the comparison. Sample size (n) is number of offspring.

4.4.4 Offspring rearing or parental temperature had little influence on offspring sex ratios

Offspring reared in 28.5°C of control parents (♂♀) had a median ratio of 0.53 males, as expected (table 4.1). Offspring sex ratios were skewed in some treatments, for example the most consistent and largest effects were 7-17% median decreases in males across the offspring rearing temperatures when fathers developed in +1.5°C, mothers developed in control, and reproduction was in control temperature (♂♀) compared to the respective offspring rearing temperatures of control parents (♂♀; table 4.1). However, parent and offspring temperatures only explained 2% of the total variation in sex ratios (i.e. marginal r^2). Furthermore, only 4% of the total variation in sex ratios was explained when also including the random effects (i.e. conditional r^2) such as paternal and maternal family effects, F1 pair, and F2 rearing tank.

Table 4.1 Offspring sex ratios. Bayesian posterior medians and 95% highest posterior density credible intervals (CI) of offspring being male at approximately three months post hatching from each parental (F1) and offspring (F2) temperature. Posterior probabilities (i.e. confidence) of a male or female bias are expressed as a percent with the comparison to the respective offspring rearing temperature (28.5°C, 29.25°C, or 30°C) of control parents (♂♀). Within control parents (♂♀), the posterior probabilities for offspring reared in 29.25°C and 30°C are relative to sibling offspring reared in 28.5°C.

F1 temperature	F2 temperature	*n*	Median ratio (male)	95% CI	Probability male bias	Probability female bias
	28.5°C	263	0.53	0.42-0.62	NA	NA
♂♀	29.25°C	264	0.49	0.39-0.59	18%	82%
	30°C	271	0.58	0.49-0.68	88%	12%
	28.5°C	128	0.45	0.32-0.57	13%	87%
♂♀	29.25°C	133	0.42	0.30-0.54	18%	82%
	30°C	142	0.41	0.29-0.54	1%	99%
	28.5°C	287	0.49	0.39-0.60	29%	71%
♂♀	29.25°C	279	0.50	0.38-0.60	56%	44%
	30°C	264	0.57	0.47-0.67	43%	57%
	28.5°C	140	0.51	0.39-0.63	39%	61%
♂♀	29.25°C	127	0.56	0.42-0.69	84%	16%
	30°C	137	0.53	0.41-0.66	23%	77%
	28.5°C	197	0.51	0.40-0.62	38%	62%
♂♀	29.25°C	210	0.44	0.33-0.55	25%	75%
	30°C	200	0.55	0.44-0.66	28%	72%
	28.5°C	116	0.64	0.52-0.78	92%	8%
♂♀	29.25°C	121	0.53	0.40-0.66	73%	27%
	30°C	109	0.55	0.41-0.68	35%	65%

The father and mother's developmental temperature is represented by sex symbols and the reproductive temperature by an egg and sperm icon whereby blue denotes present-day control temperature and orange a temperature increase of 1.5°C. Sample size (n) is number of offspring.

4.5 Discussion

My results show that the morphology of a coral reef fish is affected by its rearing temperature and the developmental and reproductive temperatures of its mother and father. As expected, offspring of parents exposed to present-day control temperatures reared in warmer water were shorter than their siblings reared in control temperature; however, within-generation plasticity allowed them to maintain their weight, which resulted in a higher condition. A higher body condition may increase predator evasion, competitive ability, and thermal tolerance and therefore could be adaptive (Booth & Hixon, 1999; Grorud-Colvert & Sponaugle, 2006; Poulos & McCormick, 2015; Robinson, Gomez-Raya, Rauw, & Peacock, 2008). By contrast, parental

exposure to warming, irrespective of ontogenetic timing and sex, resulted in lighter and lower condition offspring in all rearing temperatures, i.e. carry-over parental effects. Reduced weight and condition are generally thought to be maladaptive (Booth & Beretta, 2004; Booth & Hixon, 1999; Goatley & Bellwood, 2016; Grorud-Colvert & Sponaugle, 2006; Meekan et al., 2006), however, combined with previous studies in *A. polyacanthus* they could be the result of an adaptive parental effect on metabolism (Donelson, Munday, McCormick, et al., 2012; Munday et al., 2016). Consequently, warm-exposed parents may produce offspring that maintain their metabolic rate in ambient elevated temperatures, but at a cost of reduced weight and subsequent loss of condition since length was typically maintained. Conversely, offspring sex ratios were not strongly influenced by their rearing temperature or that of their parents. Importantly, family-level effects were minimal in all traits, indicating that the observed phenotypic changes in the present study are unlikely to be the result of differential performance among genotypes. These results show the overriding influence parental effects may have on within-generation plasticity. Further they highlight the potential trade-offs of plasticity within and between generations.

Within-generation plasticity resulted in slightly shorter fish that maintained their weight and accordingly were in better condition with increasing temperature. Metabolic rates of ectotherms increase with rising temperature (Gillooly et al., 2001; Pörtner & Knust, 2007). Given that the energetic resources (e.g. yolk provisioning and food) were equal across offspring rearing temperatures from control parents, it seems length was sacrificed while weight was maintained thus increasing condition. Offspring reared in +0.75°C (29.25°C) had approximately half the amount of phenotypic change of offspring reared in +1.5°C (30°C), suggesting that the plasticity effect size scales with temperature. Increasing physical condition with warming during development has been observed previously in *A. polyacanthus* and other damselfishes (Donelson, 2015; Donelson et al., 2014; Donelson, Munday, McCormick, et al., 2012; Grenchik et al., 2013). Furthermore, natural latitudinal thermal gradients show that as water temperature increases above ~28.5°C, larval growth and length at settlement decreases in some reef fishes (McLeod et al., 2014). However, maintenance of condition may not be a consistent pattern across reef fishes, as wrasses reared in warmer water were shorter, lighter and lower in body condition (Motson & Donelson, 2017). It may be that for some reef fishes, high condition is beneficial in elevated temperatures as it can increase predator evasion, competitive ability, and enhance thermal tolerance (Booth & Beretta, 2004; Booth & Hixon, 1999; Grorud-Colvert & Sponaugle, 2006; Robinson et al., 2008), thus this within-generation plastic response could be adaptive. Since food availability can influence the impact of temperature (Donelson, Munday,

& McCormick, 2012; Donelson et al., 2010; Munday et al., 2008), it is likely that by providing juveniles in this experiment with ample food it allowed the observed maintenance of weight and increasing condition. Maintenance of weight and physical condition may be more variable in natural populations compared with the laboratory experiments conducted here due to the temporal and spatial variation in food supply in the wild, especially as the oceans warm (Munday et al., 2009).

Parental effects were observed with parental exposure to warming decreasing offspring weight and condition relative to offspring of parents exposed solely to present-day temperature. Reduced offspring weight and physical condition at three months post-hatching was observed regardless of when the parents were exposed to warming (development and/or reproduction) and whether the mother, father, or both parents were exposed. The parental effects were similar across offspring rearing temperatures, which suggests they are carry-over effects (Bonduriansky & Crean, 2018; Jablonka et al., 1995). A lower weight may be considered adaptive in water-breathing animals due to an increase in heat tolerance (Forster et al., 2012; Leiva et al., 2019), but this is dependent on maintaining body condition (Robinson et al., 2008), which was not the case for progeny from warm-exposed parents. Therefore, it seems unlikely that lighter and lower condition juveniles had higher heat tolerance. Furthermore lighter and lower condition individuals may have a higher predation risk and reduced competitive ability (Booth & Beretta, 2004; Booth & Hixon, 1999; Goatley & Bellwood, 2016; Grorud-Colvert & Sponaugle, 2006; Meekan et al., 2006; Poulos & McCormick, 2015; Shima & Swearer, 2010). Alternately, the decrease in offspring weight and subsequent decline in condition may be genetically linked to an adaptive parental effect on metabolism. Previous studies have shown that *A. polyacanthus* offspring from warm-exposed parents increased their maximum metabolic rate and thus restored their aerobic scope at elevated temperatures and both these traits showed negative genetic correlations with body weight (Donelson, Munday, McCormick, et al., 2012; Munday et al., 2016). Together, these results illustrate the complex trade-offs between traits that may occur and the difficulty of identifying the potential adaptive or maladaptive nature of plastic changes.

Differences in offspring weight at hatching did not simply carry through to three months of age, as hatching weight was similar in all parental groups that reproduced at control temperature. When parents reproduced at +1.5°C, newly hatched offspring were either shorter or lighter, which is not surprising given embryos developed in the same elevated temperature as their parents and warming can increase developmental rates (Chapter 3; Sheridan & Bickford, 2011). Alternatively, smaller hatchlings may be the result of stressed parents devoting less

energy to embryonic care (Spatafora, Massamba N'Siala, Quattrocchi, Milazzo, & Calosi, 2021; Wiley & Ridley, 2016). Nevertheless, by three months post hatching it did not seem to matter whether parents had been exposed to higher temperature during development or reproduction; offspring were lighter and in lower condition either way. Development has been previously revealed as a crucial period to induce beneficial plasticity within and between generations (Chapters 2 and 3; Donelson & Munday, 2015; West-Eberhard, 2003), yet my findings suggest the ontogenetic timing of exposure to warming in the parental generation does not have a significant effect on offspring weight and condition at three months post hatching. Interestingly, while additive effects of developmental and reproductive exposure to warming were observed in terms of a substantial decline in reproduction from females and reduced reproductive output from males (Chapter 3), here there were no increased phenotypic effects to offspring growth with combined paternal developmental and reproductive exposure. Perhaps these fathers adaptively reduced the number of progeny to prevent lasting carry-over effects from extended paternal exposure to warming.

While parental exposure to warming generally decreased offspring weight and condition, there were some differences due to paternal and maternal timing of exposure. Interestingly, pairs where fathers developed in +1.5°C, mothers developed in present-day temperature, and reproduction was in present-day temperature, offspring were shorter at three months post hatching, in addition to decreased weight and condition. This developmental paternal effect is likely a trade-off, similar to that observed for within-generation plasticity, whereby individual length is reduced to lessen the impact on physical condition. Evidence for environment-induced paternal effects on offspring size is increasing (e.g. Bonduriansky & Head, 2007; Northstone, Golding, Smith, Miller, & Pembrey, 2014; Shama & Wegner, 2014). For instance, low condition male guppies were shown to produce poor quality sperm and consequently had smaller sized offspring (Evans et al., 2017). Since *A. polyacanthus* exhibits biparental care of embryos, there may be even greater opportunity for fathers to influence offspring size. However, I did not observe the same reduction in juvenile length when +1.5°C fathers paired with control mothers and instead reproduced in +1.5°C. The only other parental group where there was a reduction in offspring length at three months was mothers and fathers that developed in present-day control temperature but reproduced in +1.5°C, although this was likely due to offspring hatching at a shorter length. One possible explanation for the pattern of reduced weight and condition, but not standard length, in the two parental treatments where mothers developed in +1.5°C and one parental treatment where fathers were continually exposed to +1.5°C is that these groups all had increased yolk at hatching compared to progeny

from control parents. It is possible that the extra yolk allowed these offspring to maintain length or perhaps more hormones were transmitted via maternal provisioning (Dantzer et al., 2013; Gagliano & McCormick, 2007; McCormick, 1999; Uller, Astheimer, & Olsson, 2007; Warner & Lovern, 2014).

Exposure of offspring or parents to warming did not strongly skew offspring sex ratios. Offspring reared in present-day temperature from parents exposed solely to present-day temperature produced the expected 1:1 sex ratio for *A. polyacanthus*. Intriguingly, I observed no sex bias when siblings were reared at 0.75°C and 1.5°C above summer average temperatures from hatching. Mixed results of the impact of developmental warming on sex determination have been observed in populations of *A. polyacanthus* from similar collection locations. Specifically, a significant male bias was found when fish were reared from hatching in +1.5°C (mean proportion males 0.66) and +3°C (mean proportion males 0.72 and 0.90) (Donelson & Munday, 2015; Rodgers et al., 2017), however, in other experiments no sex bias was observed in +1.5 and +2°C rearing treatments (Chapter 2; Rodgers et al., 2016). Given previous and current findings, it seems likely that a thermal threshold of sex bias exists around 1.5°C above present-day temperature, which may vary genetically within and among populations of *A. polyacanthus*. This is not surprising since sex can be determined by an interaction of genetics and environmental temperature in fishes (Ospina-Álvarez & Piferrer, 2008). It is also possible that diurnal temperature variation, as was included in the present study and Chapter 2 but not previous studies, may reduce the effect of warming on sex determination. Similarly, parents exposed to warming generally had little influence on offspring sex ratios. The only consistent trend from parental exposure was slightly more daughters were produced by fathers that developed in +1.5°C, mothers that developed in present-day control temperature, and reproduction was in control temperature. Interestingly, offspring were smallest from fathers only developmentally exposed to warming, therefore it may be that these fathers were in poor condition resulting in female biased offspring as observed in anole lizards (Cox, Duryea, Najarro, & Calsbeek, 2011). Sex allocation theory predicts that parents in poor condition should invest in the sex that is less costly to produce or the sex that results in enhanced fitness in those conditions (Trivers & Willard, 1973). Yet *A. polyacanthus* are sexually monomorphic so it's difficult to think of a sex-specific cost or advantage. Furthermore, parental and offspring temperatures combined only explained a small amount (2%) of the total variation in offspring sex ratios, suggesting that any bias was stochastic and not actually driven by the temperature treatments (or family, pair, and offspring rearing tank as these only explained a further 2% of total variation).

Within-generation plasticity increased physical condition at elevated temperature in a coral reef fish. Conversely, parental exposure to warming resulted in offspring with reduced weight and condition, irrespective of the parents' ontogenetic timing of exposure to warming and sex. As explained above, this carry-over parental effect might be genetically linked to an adaptive parental effect on metabolism (Donelson, Munday, McCormick, et al., 2012; Munday et al., 2016), highlighting the possible trade-offs between traits of adjusting to warming across generations and the interplay between plasticity and evolution. Nevertheless, there is some evidence that maternal provisioning may reduce the effects of paternal warming on the juveniles' length. By contrast, sex ratios were typically not influenced by elevated temperatures or that of their parents, and combined with previous work may suggest the threshold of sex bias in this species is around 1.5°C above summer average temperature and interacts with genetic sex determination. Together, my findings show that within-generation plasticity and parental effects in a warm ocean can influence individual performance and result in trade-offs between traits, all of which may translate to effects on population sustainability.

Chapter 5 Maternal and Paternal Transgenerational Plasticity to Warming Increases Swimming Speed in a Marine Fish

5.1 Abstract

Transgenerational plasticity occurs when the parental environment alters the phenotypes of future generations in both adaptive and non-adaptive ways. When adaptive, it can potentially buffer organisms against the effects of rapid climate change. Yet the relative non-genetic contributions of mothers and fathers to offspring phenotypes, and how they interact with offspring environments, are poorly understood. Here, I tested how maternal, paternal, and biparental developmental exposure to elevated temperature (+1.5°C) influenced offspring swimming performance in a coral reef damselfish (*Acanthochromis polyacanthus*). I used a full factorial design, whereby parents developed in a present-day control temperature, or mothers, fathers, or both parents developed in an elevated temperature consistent with projected marine heatwaves and average ocean warming. Parents were shifted to present-day control temperature at maturity. Offspring were raised in control, +0.75°C, and +1.5°C temperatures and their swimming performance was tested at the average summer temperature (control: 28.5°C), +0.75°C (29.25°C), and +1.5°C (30°C). As expected, juvenile fish swam faster in warmer ambient water. Moreover, there was evidence for within-generation plasticity, with offspring reared in +0.75°C from parents exposed to present-day control temperature swimming faster than their siblings reared in control temperature. Strikingly, offspring of mothers or fathers independently exposed to warming swam faster than juveniles where both parents developed in present-day temperature, or where both parents developed in warm conditions. I argue this increase in swimming speed may be a maladaptive transgenerational response to thermally mismatched parents. By contrast, offspring from thermally matched parents maintained a swimming speed that is likely optimal for the energy budget of the whole animal. Generally, the faster swimming offspring from parents with mismatched thermal histories developed in present-day temperature, suggesting the parental legacy is strongest when there is no change in temperature between the parental breeding and juvenile stages. These results highlight the importance of disentangling the relative maternal and paternal non-genetic contributions since they would have been masked if only biparental exposure was studied. They also draw attention to the complex and potentially non-adaptive ways transgenerational plasticity may be induced in response to rapid climate change.

5.2 Introduction

The environment of previous generations can influence the current generation. Specifically, the environment experienced in one generation can lead to the transfer of non-genetic information to the next generation that alters performance in either the same or different environmental conditions. The transfer of non-genetic information across generations may occur through epigenetics (e.g. DNA methylation, histone modification, or small non-coding RNAs), hormones, nutrients, cell structures, or behaviours, and can be viewed as an extension of (within-generation) phenotypic plasticity, whereby a genotype produces different phenotypes in different environments (Bonduriansky et al., 2012; Ho & Burggren, 2010). When the parental environment is predictive of the offspring environment, parents may improve the performance of their offspring in that environment, which is often referred to as adaptive transgenerational plasticity (Bonduriansky & Crean, 2018; Burgess & Marshall, 2014; Donelson et al., 2018; Uller, 2008). Likewise, if the parental experience does not effectively predict the offspring environment, it could result in maladaptive transgenerational plasticity. When transgenerational plasticity is adaptive, it can buffer organisms against rapidly changing environments as it may act much more rapidly than adaptation by natural selection (Donelson et al., 2018; Klironomos et al., 2013).

Transgenerational plasticity may be induced by the environmental experience of mothers, fathers, or both parents. Maternal contributions have long been recognised as a significant source of non-genetic phenotypic variation in a variety of taxa, arising from differences in embryonic nutritional provisioning (Mousseau & Fox, 1998). For example, mothers may match the phenotype of their offspring to changes in the local environment like seed beetles do by laying larger eggs on thick-coated seeds to provide extra resources for offspring to successfully bore through (Fox et al., 1997). Furthermore, mitochondria are typically maternally inherited and, being the powerhouse of life, they can have important implications on fitness (Ghiselli & Milani, 2020). Paternal contributions, however, are often assumed to be absent (e.g. Ernsting & Isaaks, 1997; Fischer, Brakefield, & Zwaan, 2003; Kruuk, Livingston, Kahn, & Jennions, 2015; Marshall, 2008) or much less important than maternal contributions, especially in organisms that lack conventional paternal provisioning and care (Crean & Bonduriansky, 2014). But the contribution of fathers to their offspring's phenotype is not restricted to genes alone, and non-genetic contributions via the paternal line seems increasingly likely (Crean et al., 2013; Yin et al., 2019). For instance, prepubescent smoking in men may contribute to obesity in sons, possibly through inheritance of altered epigenetic marks (Nilsson,

Sadler-Riggleman, & Skinner, 2018; Northstone, Golding, Smith, Miller, & Pembrey, 2014; Pembrey et al., 2006).

Sex-specific transgenerational plasticity is most likely to evolve when males and females have different reproductive strategies (Burke et al., 2020) or patterns in socialising, foraging, predation, or parasitism (Lewis et al., 2002; Magnhagen, 1991; Ruckstuhl, 2007; Zuk & McKean, 1996). But even when the sexes are alike and both parents provide non-genetic contributions to offspring, it is possible that mothers and fathers experience different environments when temporal environmental variation exists and breeding pairs are of mixed age (Mills, 1973) or large spatial areas are traversed (Shimada et al., 2020). This could lead to differing maternal and paternal non-genetic contributions to offspring phenotypes. Accordingly, while transgenerational experiments with biparental exposure to environmental stressors are important, studies should also seek to disentangle the relative roles of mothers and fathers (Burke et al., 2020; Donelson et al., 2018). In fact Burke et al. (2020) suggests the lack of sex-specific studies has masked evidence of transgenerational plasticity. Understanding whether mothers, fathers, or both parents influence offspring phenotypes will improve mechanistic insight and help establish the extent of transgenerational plasticity in animal populations.

Transgenerational plasticity can be adaptive when the parental environment successfully predicts the offspring environment, but it's unclear whether both the maternal and paternal environments are important. Transgenerational plasticity is often adaptive when offspring experience the same environmental stressor as their parents (Crean et al., 2013; Marshall & Uller, 2007), but may be costly to offspring performance when conditions differ from those experienced by parents (Ghanizadeh Kazerouni, Franklin, & Seebacher, 2017; Jensen, Allen, & Marshall, 2014). An unresolved question is what happens when only one parent is exposed to an environmental stressor, meaning there is a mismatch between the experience of mothers and fathers? The answer will likely depend on whether transgenerational plasticity is sex-specific or both parents contribute to offspring phenotype. For instance, if mothers are the sole contributor of transgenerational plasticity, and the mother's environment is a good predictor of the offspring's environment, we would expect an improvement in offspring performance. Alternatively, if both parents contribute to transgenerational plasticity, we may see improvement in offspring performance if their environmental experience is consistent with just one parent, but it's also possible the mismatch in environmental experience between parents has consequences (Lehto & Tinghitella, 2020). When offspring conditions match to both parents' environment, it's possible offspring performance is optimised beyond that of

mothers and fathers independently exposed (Jensen et al., 2014). Owing to logistical challenges, rarely do transgenerational experiments disentangle the relative non-genetic roles of mothers and fathers and explore potential interactions across a range of offspring environments (for exceptions see Hellmann, Bukhari, et al., 2020; Jensen et al., 2014; Shama et al., 2016). In fact, such experimental designs are almost absent in a climate change context. Understanding how the mother, father, or biparental environment interacts with the offspring environment is important for determining the selective forces acting on transgenerational plasticity and to accurately predict how populations will adjust to environmental change over multiple generations.

Due to the rapid rate of warming projected to occur over the coming decades, transgenerational plasticity is expected to be a critical mechanism by which animals might adjust their performance across generations to help cope with warmer conditions (IPCC, 2013; Munday et al., 2013). The physiological performance of tropical ectotherms, like coral reef fishes, is tightly linked to environmental temperature and, because they live close to their thermal maximum, they are susceptible to small temperature increases (Pinsky et al., 2019; Sunday et al., 2011; Tewksbury et al., 2008). Increased water temperature can affect metabolic rates (Nilsson et al., 2009), activity patterns (Johansen et al., 2014), escape responses (Allan et al., 2015), developmental rates (Green & Fisher, 2004), growth (Munday, Kingsford, et al., 2008), sex ratios (Donelson & Munday, 2015), and reproduction (Miller et al., 2015) of coral reef fishes. Transgenerational plasticity has been shown to partially or fully mediate the negative effects of warming (+1.5-3°C) in a coral reef damselfish (*Acanthochromis polyacanthus*) on traits such as metabolism, sex ratios, and reproduction (Donelson & Munday, 2015; Donelson, Munday, McCormick, et al., 2012; Donelson et al., 2016), but we do not know the relative roles of mothers and fathers as these previous experiments investigated biparental transgenerational plasticity (but see Chapter 3). Furthermore, it's unknown if swimming performance, critical to the success of fishes (Plaut, 2001), is transgenerationally plastic in warming scenarios. Critical swimming speed is a robust and well-established performance metric in fishes that positively correlates with the maximum capacity for oxygen uptake (Brett, 1964; Fisher, Leis, Clark, & Wilson, 2005; Norin & Clark, 2016; Plaut, 2001). It measures the maximum prolonged swimming speed fish may use to avoid predators, evade unfavourable conditions, or feed in a current, and is estimated by increasing water velocity in a swim tunnel incrementally until the fish fatigues (Plaut, 2001). Generally, critical swimming speed increases with temperature owing to reduced viscosity of the water and an increase in the activity of swimming muscles, but will decline as temperatures approach the upper thermal limits (Claireaux, Couturier, & Groison,

2006; Downie, Illing, Faria, & Rummer, 2020; Hunt von Herbing, 2002; Johansen & Jones, 2011). Consequently, the energetic costs of maximal swimming in elevated temperature on coral reef fishes can be high (Johansen & Jones, 2011). A critical aspect of understanding the effects of warming on coral reef fishes yet to be explored is whether mothers and fathers can influence offspring critical swimming speed.

Here I investigated maternal, paternal, and biparental transgenerational plasticity of swimming performance at elevated temperatures in a coral reef damselfish, *Acanthochromis polyacanthus* (Bleeker 1855). Specifically, I reared males and females at the present-day average temperature for their population (control), or at 1.5°C above the average temperature, consistent with climate change projections and heatwaves that are already occurring in marine ecosystems (Frölicher et al., 2018; IPCC, 2019). I created adult breeding pairs that consisted of: 1) both males and females developed in control (♂♀), 2) only females developed in +1.5°C (♂♀), 3) only males developed in +1.5°C (♂♀), or 4) both males and females developed in +1.5°C (♂♀). I reared their offspring in present-day average summer temperature (control), +0.75°C and +1.5°C until three months and then measured critical swimming speed at the average summer temperature (28.5°C), +0.75°C (29.25°C), and +1.5°C (30°C). I replicated this across multiple families. This experimental design allowed me to determine acute effects, within-generation plasticity, maternal and paternal transgenerational plasticity, and family (i.e. mostly genetic) effects of high temperature exposure on critical swimming speed. *A. polyacanthus* is common on reefs in the Indo-Australian archipelago. They lack a dispersal larval stage and adults are site attached with small home ranges (Miller-Sims et al., 2008; Robertson, 1973). They form monogamous pairs, breed primarily during the summer months and provide biparental care (Kavanagh, 2000; Pankhurst et al., 1999). Therefore *A. polyacanthus* are unlikely to migrate to more favourable environments under climate warming, including to deeper waters. In natural populations differing maternal and paternal thermal histories would most likely occur with mixed age pairs where one parent developed during a marine heatwave and the other during a year of usual sea temperature. I hypothesised that 1.5°C higher temperature would allow *A. polyacanthus* to swim faster, because this temperature increase is likely within the study population's thermal limits, and that both within-generation plasticity and transgenerational plasticity would be present. I expected both mothers and fathers to play a role in transgenerational plasticity and sons and daughters to perform equally owing to their reproductive strategy. I also predicted an interaction between the parent and offspring environment, whereby matching mother, father, or biparental temperature with offspring temperature would be beneficial.

5.3 Methods

5.3.1 Experimental design

Two generations of *A. polyacanthus* were reared in environmentally controlled conditions to examine temperature-induced transgenerational plasticity. Detailed descriptions of the F0-F2 generations and the aquaria facilities are provided in Chapters 3 and 4. Briefly, to account for genotypic variation, I began the experiment with six wild-caught pairs from the Palm Islands region (18° 37′ S, 146° 30′ E) of the central Great Barrier Reef (F0 generation figure 5.1). Pairs were provided half a terracotta pot as a spawning site. In the Austral summer of 2016, the F0 generation bred. Egg clutches were kept with the parents until hatching, allowing them to provide nest care as occurs in the wild. Newly hatched F1 generation siblings were divided between a present-day control and +1.5°C temperature treatment with 10 fish per tank and a minimum of five replicate tanks per clutch (figure 5.1). A 1.5°C increase already occurs on the Great Barrier Reef during marine heatwaves (Chapter 2; Frölicher et al., 2018; Hughes et al., 2019) and is projected to be the average temperature increase by 2050 – 2100 (IPCC, 2013). The control water temperature simulated seasonal (winter minimum 23.2°C, summer maximum 28.5°C) and diurnal (0300hrs -0.6°C, 1500hrs +0.6°C) cycles for the Palm Islands region based on temperature loggers from 2002 to 2015 at 0.2-14.6m depth (AIMS, 2016), with the elevated treatment matching this, but 1.5°C higher. Similarly, the photoperiod of the Palm Islands region was replicated, reaching a maximum of 13h 15min light in summer (December) and a minimum of 11h 01min light in winter (June). Seasonal changes to water temperature and illumination were adjusted weekly.

In the Austral winter of 2017, the F1 generation reached maturity and were paired so that: 1) both males and females developed in control (♂♀), 2) only females developed in +1.5°C (♂♀), 3) only males developed in +1.5°C (♂♀), or 4) both males and females developed in +1.5°C (♂♀). I crossed males and females of one family with another following figure 1A in Bonduriansky, Crean, and Day (2012) such that I had three family crosses from the original six F0 families. This resulted in approximately 20 pair replicates for each parental temperature inclusive of families (Chapter 3). After pairing in winter all fish were maintained in control conditions until breeding in summer to ensure that phenotypic changes in offspring were not due to early developmental effects of higher temperature on developing gametes or embryos (figure 5.1). In the Austral summer of 2017/2018, the F1 generation bred in similar proportions across three of the parental treatments and all family crosses, with slightly more pairs breeding when mothers developed in +1.5°C (Chapter 3).

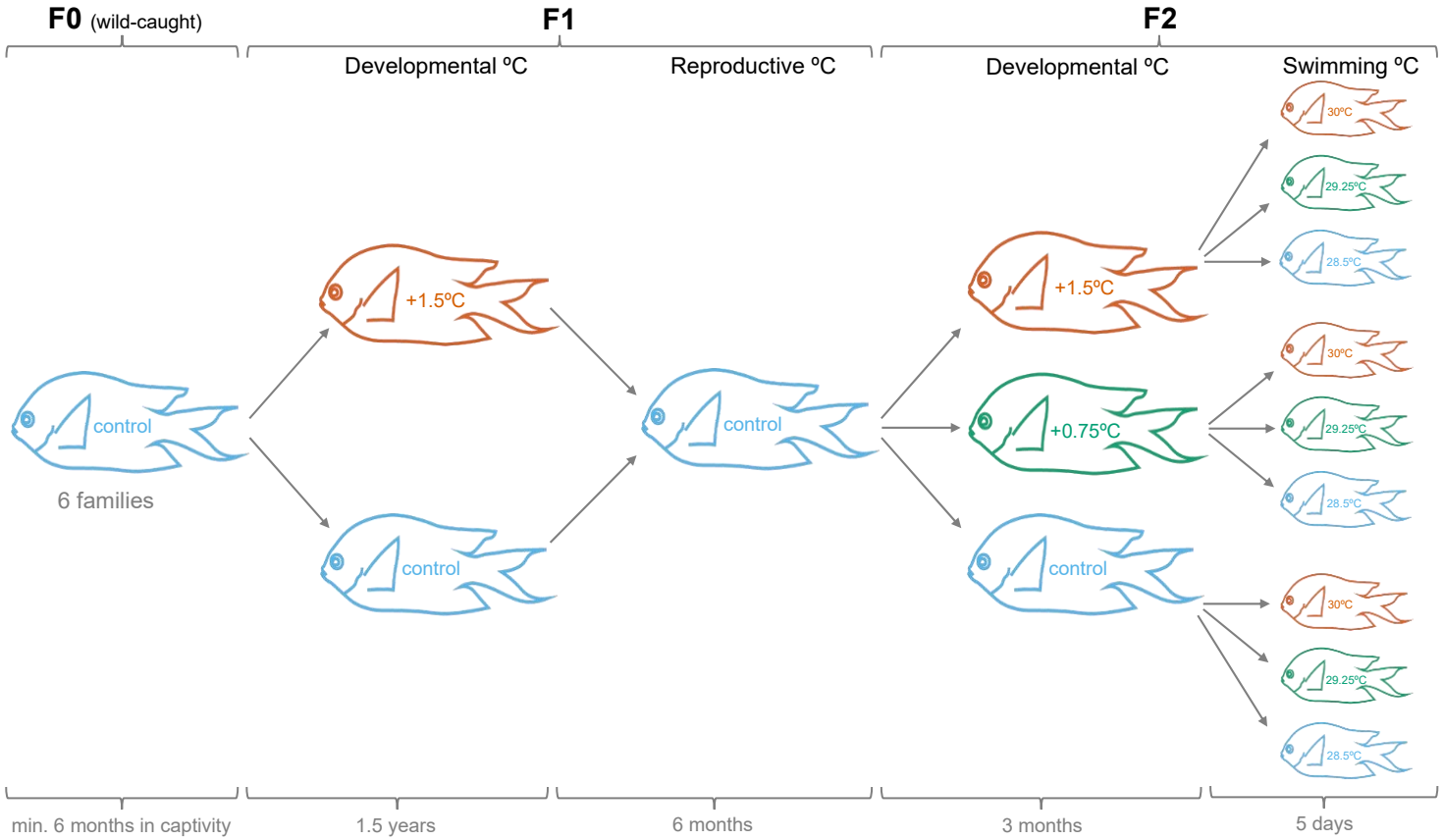

Figure 5.1 Experimental design. Newly hatched A. polyacanthus from six wild-caught families were split between a present-day average temperature for their population (control) and 1.5°C above the average temperature. At maturity the F1 generation were placed in control conditions during winter and paired for breeding in summer so that neither sex, only females, only males, or both sexes developed in +1.5°C. Newly hatched siblings (F2 generation) were split among a present-day average summer temperature (control), +0.75°C, and +1.5°C. At approximately 3 months, I tested the F2 generation's swimming performance at the average summer temperature (28.5°C), 29.25°C (+0.75°C), and 30°C (+1.5°C).

Newly hatched F2 generation siblings were split among a present-day average summer temperature control (28.5°C), +0.75°C (29.25°C), and +1.5°C (30°C) temperature, per clutch this was 20 fish in a tank across two replicate tanks for each temperature treatment (figure 5.1). I incorporated +0.75°C as it is a half-way point between potentially favourable and unfavourable thermal environments. Manipulating both parent and offspring environments across a range of ecologically relevant temperatures provides the opportunity to detect within-generation plasticity and transgenerational plasticity (Bonduriansky & Crean, 2018; Donelson et al., 2018). Each temperature treatment had a daily temperature cycle of ±0.6°C matching the natural diurnal temperature variation experienced by this inshore population in the wild (AIMS, 2016). Hatchlings were given 2–3 hours to slowly equilibrate to their rearing temperature via a 2 L tub floated in the tank and receiving gradual inflow. Hatchlings were fed live *Artemia nauplii* and then weaned to commercial pellets (Chapter 3). Offspring were grown to three months of age when the swimming performance of 3-5 clutches per parental temperature was measured. To determine the acute effects of high temperature on swimming speed, fish were swum at 28.5°C, 29.25°C, or 30°C (figure 5.1; Schulte, Healy, & Fangue, 2011). To prevent a thermal stress response, offspring were acclimated to their swimming temperature a minimum of five days before trials.

5.3.2 Swimming performance

Critical swimming speed was determined in the F2 generation using a five-lane swim tunnel as described by Stobutzki and Bellwood (1997), that has been widely used (e.g. Bignami, Sponaugle, & Cowen, 2013; Faria, Ojanguren, Fuiman, & Gonçalves, 2009; Fisher et al., 2005; Munday, Donelson, Dixson, & Endo, 2009; Watson et al., 2018) and shown to be reliable in measuring critical swimming speed (Illing et al., 2020). Each lane was 180 L x 30 W x 50 H mm. Swim tunnel water speed was calculated by dividing the distance the water travelled (i.e. volume of water flowing over the weir divided by the cross-sectional area of the tunnel) by a unit time (Faria et al., 2009). Water speed was calibrated by a gate value mounted with a protractor and angled so that degrees correspond with a given speed (Stobutzki & Bellwood, 1994; Watson et al., 2018). Swim tunnels were calibrated several times during the study. I confirmed lanes had the same speeds and laminar flow using food dye (Cominassi et al., 2019). Precise temperature control was achieved by a 1 kW custom-built heater (±0.01°C, Control Distributions, Carlton, Australia) with a digital thermostat (±0.1°C, Full Gauge Controls Tic-17RGTi, Canoas, Brazil) and a chiller with an internal thermostat (±0.1°C, Hailea HC-250A, Guangdong, China)

connected to a 400 L water reservoir. Water temperature was checked regularly with a digital thermometer (±0.1°C, Comark Instruments C26, Norwich, UK).

Critical swimming speed was estimated by increasing water velocity in the swim tunnel incrementally until the fish fatigued. A total of 1132 offspring between the ages of 95-106 days post hatching (dph) were swum between March and July 2018. I tested a maximum of 10 fish per trial using two swim tunnels run concurrently and completed an average of three trials a day between 07:30 and 18:00. Swimming temperatures were randomised among trials. Swim tunnel and reservoir water was replaced daily. I fasted fish for approximately 20 hours prior to trials to ensure a post-absorptive state (Binning, Ros, Nusbaumer, & Roche, 2015; Johansen & Jones, 2011). At the start of a trial, fish were haphazardly selected and removed from their tank using a water-filled container and randomly placed in a lane using a small net. The swim tunnel lid was secured and fish were given five minutes to habituate at a water speed of 3 cm s^{-1} (~0.95 body lengths [bl] s^{-1}). Pilot trials with sibling fish not used in this experiment determined this habituation speed and time were sufficient since the juveniles displayed calm behaviour and standard gill respiration rates. Speed was then increased by 2 cm s^{-1} (~0.63 bl s^{-1}) increments, every five minutes. I considered fish fatigued when they were swept downstream and against the retaining mesh grid for >30 s (Nikora et al. 2003). Swimming trials were recorded with a video camera (Panasonic HC-V180K, Osaka, Japan) placed on a tripod directly above the swim tunnels. Time to fatigue was quantified blind from video playback. Critical swimming speed (U_{crit}) was calculated from Brett's (1964) equation:

$$U_{\text{crit}}\ (\text{cm s}^{-1}) = U + \frac{\text{t}}{\text{t}_\text{i}} U_\text{i}$$

Whereby U is the last speed before fish fatigued, t is the time elapsed in the final increment during which the fish fatigued, t_i is the amount of time maintained at each speed (5 minutes), U_i is the speed increment (2 cm s^{-1}). I then converted absolute critical swimming speed to the commonly used relative measure of bl s^{-1} (Brett, 1964; Leis, Hay, Lockett, Chen, & Fang, 2007; Plaut, 2001).

Immediately after trials, fish were sexed in a water filled clear bag under the microscope via external examination of the urogenital papilla (Hilder & Pankhurst, 2003), euthanised by cervical dislocation, weighed (±0.001 g), and standard length measured (±0.002 cm). Fish occupied an estimated 25% of the cross-section of a lane, which could mean they experienced solid blocking effects, i.e. fatter fish may be subjected to slightly faster water speed (W. H. Bell & Terhune, 1970). I couldn't apply Bell and Terhune's (1970) correction as I did not measure fish

width, instead, I present the results standardised by fish size, which is defined as weight divided by standard length. I excluded two fish prior to analysis as they displayed very dark colouration during their swimming trial, which suggests disease in captive *A. polyacanthus* (personal observation R. K. Spinks), and they swam slower than most other individuals.

5.3.3 Statistical analysis

I implemented Bayesian mixed models using the rstanarm package v. 2.21.1 (Goodrich et al., 2020) in R v. 4.0.3 (R Core Team, 2020).The dependent variable was critical swimming speed in bl s^{-1}. The independent variables were the thermal exposures of the F1 (♂♀, ♂♀, ♂♀, ♂♀) and F2 (control, +0.75°C, +1.5°C) generations, the swimming temperature (28.5°C, 29.25°C, 30°C), and their interactions. I included fish size (centered and scaled) as a covariate to adjust for solid blocking effects. This improved the model fit visually and with Bayesian leave-one-out cross-validation (LOO Vehtari, Gelman, & Gabry, 2017), albeit there were no significant changes to the results. I considered offspring sex as an independent variable (and its interactions) in the event that swimming speed differed for daughters and sons (Burke et al., 2020), but there was no obvious influence and based on model fits visually and with LOO it was omitted from the final model. The model's random intercept varied by father family (6 levels) and mother family (6 levels) due to non-independence between offspring from the same F0 family line of the father and between offspring from the same F0 family line of the mother. The random intercept also varied by F2 rearing tank (91 levels) nested in F1 pair (15 levels) due to non-independence between offspring from the same tank and offspring from the same parent. Random slopes, which varied by the thermal experiences of the F1 and F2 generations and the swimming temperature, were included with the previous random intercepts because they were biologically sensible and improved the model fit visually and with LOO. Lastly, swim tunnel lane (10 levels) was incorporated as a random intercept due to non-independence between offspring that swam in the same lane.

I modelled critical swimming speed with a Gaussian distribution and specified weakly informative priors (appendix table 5.1). Visual posterior checks confirmed that priors never heavily influenced the posterior. Using the Hamiltonian Monte Carlo algorithm, the final model was run with three chains by means of the No-U-Turn sampler for 12000 iterations with every third posterior sample thinned and the first 50% discarded. Models were validated visually and followed linear mixed model assumptions of linearity, homogeneity of variances, and normality. Bayesian model validation followed Chapter 2. In order to compare among parental

temperatures without confounding offspring swimming and rearing temperature effects, groups were compared to their respective offspring swimming (28.5°C, 29.25°C, 30°C) and rearing temperature (control, +0.75°C, +1.5°C) of control parents (♂♀). I used probability, which is to calculated from the posterior distribution, to determine statistical significance. Probabilities are expressed as a percent and the closer they are to 100% suggests greater confidence in a group swimming slower or faster relative to its comparison, whereas nearer to 50% suggests little confidence in a group swimming slower or faster relative to its comparison. Note that Bayesian inference (with suitable priors) does not require correction for multiple comparisons (Gelman & Tuerlinckx, 2000). Figures were created with the R packages' emmeans v. 1.5.1 (Lenth, 2020) and tidybayes v. 2.1.1 (Kay, 2020) and present highest posterior density credible intervals, which are analogous to Frequentist confidence intervals.

5.4 Results

5.4.1 Acute effects

Critical swimming speed increased at the higher swimming temperature. The median critical swimming speed was 7.85 bl s^{-1} for *A. polyacanthus* when parents (♂♀) and offspring developed in present-day control temperature and offspring swam in that same control temperature (28.5°C; figure 5.2). Critical swimming speed increased by a median of 8% in sibling offspring reared in control temperature and swum in 30°C (>99% probability of swimming faster, figure 5.2).

5.4.2 Within-generation plasticity

Offspring that developed in +0.75°C also swam faster. When parents developed in control temperature (♂♀), but offspring developed in +0.75°C a 4% median increase in speed was observed when juveniles swam in 28.5°C relative to offspring reared in control temperature and swam in 28.5°C (98% probability of swimming faster, figure 5.2). However, when sibling offspring developed in +1.5°C, swimming speeds were closer to those reared in control temperature given that the median increase or decrease was negligible and the probabilities of swimming faster or slower were ≤84% in the respective swimming temperatures (figure 5.2).

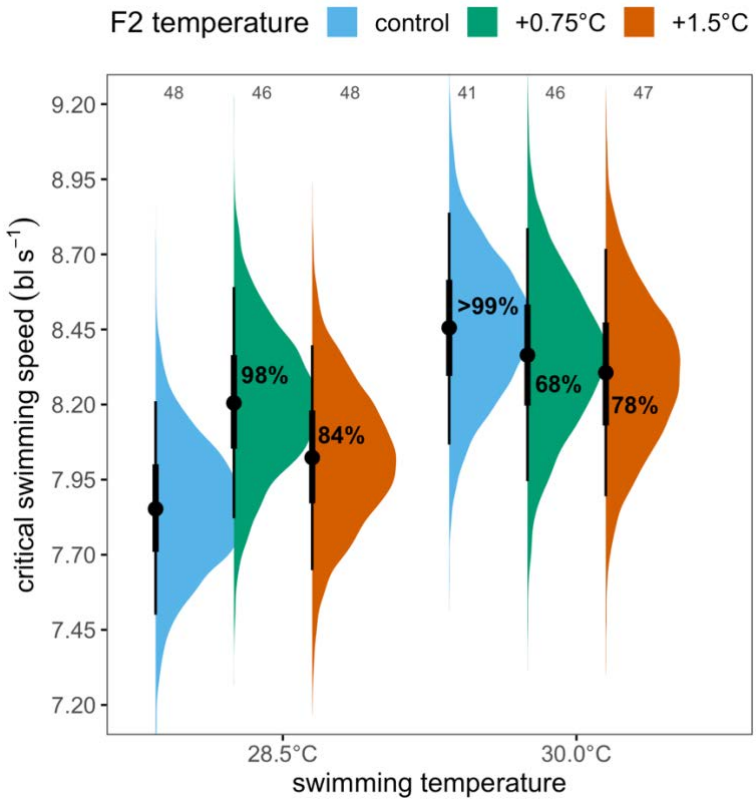

Figure 5.2 Offspring swimming performance of parents in present-day control temperature. Critical swimming speed in body lengths (bl) s^{-1} of the F2 generation swum at 28.5°C (present-day control) or 30°C (+1.5°C) and reared in present-day control (blue), +0.75°C (green), and +1.5°C (orange) temperatures from F1 generation reared in present-day control temperature (♂♀). Bayesian posterior medians (black circles), 50% credible intervals (thick black lines), 90% credible intervals (thin black lines), and density distributions are provided. The percent values above or below each median value indicate the posterior probabilities of swimming faster or slower relative to the respective swimming (28.5°C or 30°C) temperature of F2 reared in present-day control temperature (blue). The posterior probability at 30°C swimming temperature (>99%) of F2 reared in present-day control temperature (blue) is relative to 28.5°C swimming temperature of F2 reared in present-day control temperature (blue). Critical swimming speed is presented at the average fish size of 0.41 g cm^{-1}. The sample sizes for each treatment are stated at the top.

5.4.3 Transgenerational plasticity

Mother's reared in +1.5°C and father's reared in control temperature (♂♀) produced offspring with a faster critical swimming speed compared to offspring of control parents (♂♀, 94% probability of swimming faster with offspring and swimming temperatures combined).

Specifically, offspring of warm mothers (♂♀) reared in control temperature and swum in 28.5°C had a 4% median increase and 89% probability of swimming faster, and offspring swum in 30°C had a 5% median increase and 93% probability of swimming faster, relative to these swimming temperatures in offspring reared in control temperature of control temperature parents (♂♀; figure 5.3A). Offspring of warm mothers (♂♀) that were reared in +1.5°C and swum in 28.5°C also exhibited a 5% median increase and 91% probability of swimming faster relative to offspring of control parents (♂♀) reared in +1.5°C and swum in 28.5°C (figure 5.3C). By contrast, swimming speeds of +0.75°C reared offspring swum in 28.5°C and 30°C and +1.5°C reared offspring swum in 30°C were closer to the respective swimming and developmental temperatures in offspring of control parents (♂♀) given that the median increases or decreases were lower than the previously mentioned groups and the probabilities of swimming faster or slower were ≤81% (figure 5.3B, C).

Father's reared in +1.5°C and mother's reared in control temperature (♂♀) produced offspring with a faster critical swimming speed compared to offspring of control parents (♂♀, 97% probability of swimming faster with offspring and swimming temperatures combined). Specifically, offspring of warm fathers (♂♀) reared in control temperature and swum in 28.5°C had a 9% median increase and >99% probability of swimming faster, and offspring swum in 30°C had a 5% median increase and 91% probability of swimming faster, relative to these swimming temperatures in offspring reared in control temperature of control temperature parents (♂♀; figure 5.3A). By contrast, offspring of warm fathers (♂♀) reared in +0.75°C and +1.5°C and swum in 28.5°C and 30°C were closer to the respective swimming and developmental temperatures in offspring of control parents (♂♀) given that the median increases or decreases were lower than the previously mentioned groups and the probabilities of swimming faster or slower were ≤83% (figure 5.3B, C).

Swimming speeds of offspring of warm fathers (♂♀) compared to offspring of warm mothers (♂♀) were generally similar, except warm fathers (♂♀) produced faster swimming control-reared offspring swum in 28.5°C (5% median increase and 92% probability of swimming faster) and slower swimming +1.5°C reared offspring swum in 28.5°C (5% median decrease and 88% probability of swimming slower) compared to the same offspring treatments of warm mothers (♂♀).

Both parents reared in +1.5°C (♂♀) produced offspring that swam at similar speeds to offspring of control temperature parents (♂♀, 67% probability of swimming slower with offspring and swimming temperatures combined). Furthermore, offspring acute effects and

developmental pattern of warm parents (♂♀) generally reflected that of control parents (♂♀) given that the median increases or decreases were negligible and the probabilities of offspring swimming faster or slower were ≤82% in the respective swimming and developmental temperatures (figure 5.3).

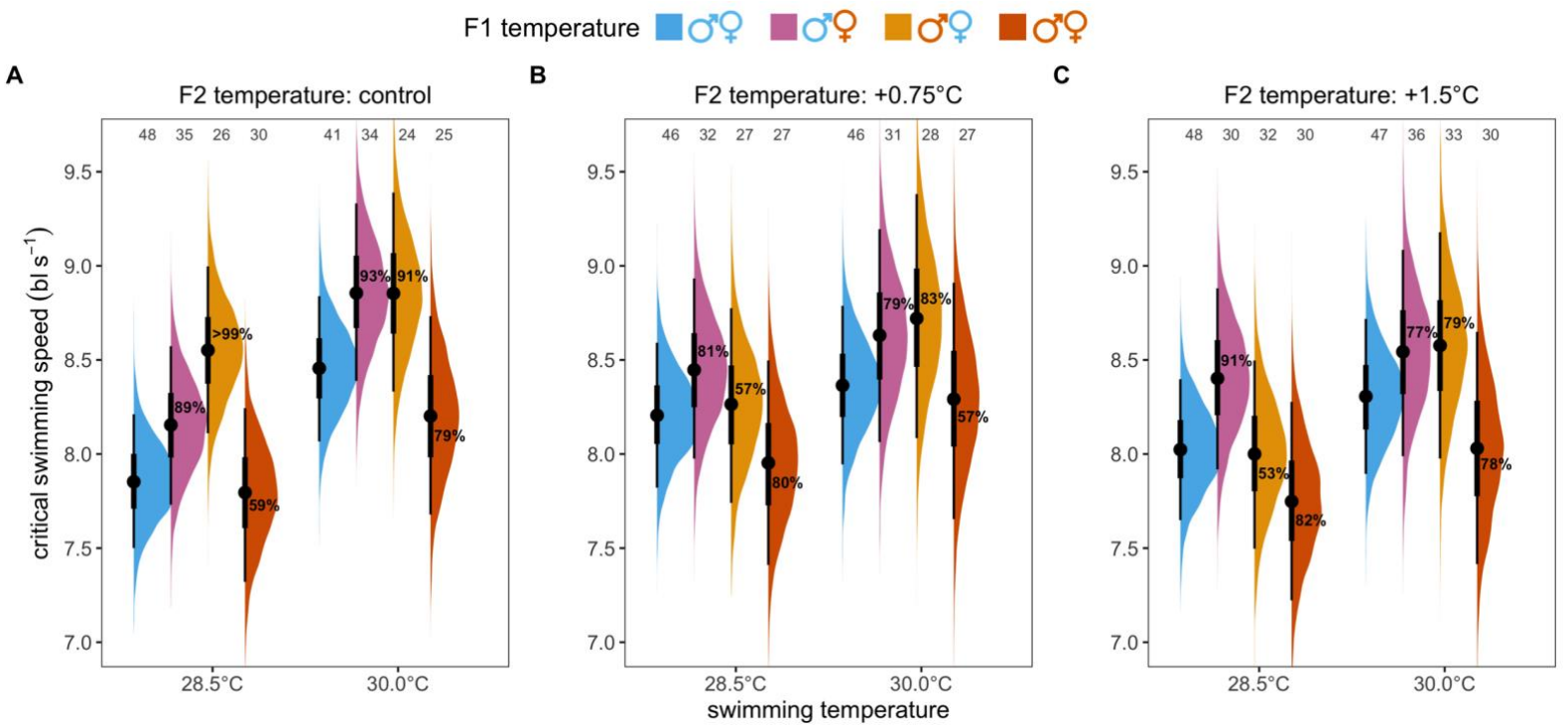

Figure 5.3 Offspring swimming performance from all parental treatments. Critical swimming speed in body lengths (bl) s^{-1} of the F2 generation swum at 28.5°C (present-day control) or 30°C (+1.5°C) and reared in A) present-day control, B) +0.75°C, and C) +1.5°C from each parental combination (i.e. F1 temperature). The F1 temperatures are 1) both parents developed in control (♂♀ - blue), 2) only mother developed in +1.5°C (♂♀ - pink), 3) only father developed in +1.5°C (♂♀ - yellow), or 4) both parents developed in +1.5°C (♂♀ - orange). Bayesian posterior medians (black circles), 50% credible intervals (thick black lines), 90% credible intervals (thin black lines), and density distributions are provided. The percent values above or below each median value indicate the posterior probabilities of swimming faster or slower relative to the respective F2 rearing (control, +0.75°C, +1.5°C) and swimming (28.5°C or 30°C) temperatures of offspring from control parents (♂♀). Critical swimming speed is presented at the average fish size of 0.41 g cm^{-1}. The sample sizes for each treatment are stated at the top.

Offspring swum in 29.25°C showed a similar pattern to the other swimming temperatures across parent and offspring temperatures (appendix figure 5.1). Variance in critical swimming speed attributed to maternal and paternal family effects were <0.003 bl s^{-1} (σ). Variance attributed to other random intercepts, e.g. F1 pairs, F2 rearing tanks, or swim tunnel lanes, and their slopes were also lower than the magnitude of parent, offspring, or swimming temperature effects. The model explained 54% (conditional r^2) of the variability in critical swimming speed with 39% (marginal r^2) owing to parent temperature, offspring temperature, swimming temperature, and fish size. Summary statistics are provided in appendix table 5.2. The same conclusions were drawn when modelling critical swimming speed as an absolute measure in cm s^{-1}.

5.5 Discussion

My results show that swimming performance of juvenile coral reef fish is affected by the ambient swimming temperature, the rearing temperature of the juveniles, and the sex-specific developmental temperature of their parents. As expected, juvenile fish swam faster in warmer water. Moreover, there was evidence for within-generation plasticity, with offspring reared in +0.75°C from parents exposed to present-day control temperature swimming faster than their siblings reared in control temperature. Finally, the developmental temperature of mothers and fathers also affected juvenile swimming performance, providing evidence for transgenerational plasticity. Offspring of mothers or fathers independently exposed to warming swam faster than juveniles where both parents developed in current-day temperature. These faster swimming offspring typically developed in current-day temperature. In nature, faster critical swimming speed may enhance a juvenile's ability to escape predators or feed in a current, but could also come at an energetic cost (Plaut, 2001; Sogard & Olla, 2002). Interestingly, when both parents were exposed to warming during development their offspring swam at similar speeds in all rearing temperatures to offspring where both parents were reared in current-day temperature. Importantly, family-level effects were minimal, indicating that these phenotypic changes are unlikely to be the result of differential performance among genotypes. Lastly, sons and daughters performed similarly under all circumstances.

Offspring of control parents swam faster when reared in +0.75°C compared to siblings reared in present-day control temperature. As expected, swimming speed increased in warmer water and provided a baseline of the acute effects of critical swimming speed in this population

of *A. polyacanthus*. When swimming in the current-day summer average temperature (28.5°C), within-generation plasticity allowed offspring reared in +0.75°C to swim faster than siblings reared in control temperature or +1.5°C. This also meant +0.75°C reared offspring had a narrower thermal performance range than control or +1.5°C reared siblings. Faster swimming speed may increase the chance of fish survival (Plaut, 2001), and could occur through increases in mitochondrial ATP production and increased efficiency in muscle function (James, 2013; Kazerouni, Franklin, & Seebacher, 2016). Alternatively, faster swimming speed could be a by-product of plastic changes to the maximum capacity for oxygen uptake since swimming performance and maximum oxygen uptake is positively correlated (Norin & Clark, 2016). This developmental flexibility follows expectations as early life stages of many taxa are more plastic than their adult counterparts (West-Eberhard, 2003). Yet enhanced swimming performance was not observed when offspring were reared in +1.5°C. Within-generation plasticity of critical swimming speed may be limited by a temperature threshold, which is further supported by a lack of plastic change to maximum metabolic rate in a similar population of *A. polyacanthus* reared in +1.5°C and +3°C (Donelson et al., 2011; Donelson, Munday, McCormick, et al., 2012). Limits to within-generation plasticity have been observed with elevated temperatures in a range of taxa and traits (e.g. Grenchik et al., 2013; Iossa, Maury, Fletcher, & Eady, 2019; Murren et al., 2015; Stillwell & Fox, 2005).

Mothers or fathers independently exposed to warming during development produced faster swimming offspring compared to offspring where both parents developed in current-day or elevated temperature. My results follow expectations that both mothers and fathers contribute to offspring phenotypes since *A. polyacanthus* is a morphologically identical, monogamous species with biparental care. Yet strikingly, when both parents developed in elevated temperature their progeny swam at similar speeds to offspring with both parents reared in current-day temperature. Although the combined effects of mothers and fathers is often additive (Hunt & Simmons, 2000; Jensen et al., 2014), there are exceptions. For example, maternal and paternal predator exposure in stickleback fish (*Gasterosteus aculeatus*) independently yielded daughters who preferred less conspicuous males, but when both parents were predator exposed a reverse in these mate preferences was observed (Lehto & Tinghitella, 2020). Furthermore, non-additive interactions between mothers and fathers on offspring gene and methylation expression profiles were observed in sticklebacks (Hellmann, Bukhari, et al., 2020) and humans (Yehuda et al., 2014), with distinct changes in offspring when both parents were exposed to predators/holocaust compared to offspring with independently exposed mothers or fathers. In my study, all parents were shifted to present-day temperatures six months

prior to breeding season, therefore sperm production and maturation of oocytes would have occurred at present-day temperature (Pankhurst et al., 1999; J. Donelson, personal communication). My results indicate that environmentally induced epigenetic changes are occurring during the parents' development, likely to the primordial germ cells (Heard & Martienssen, 2014). For mismatched parents these epigenetic changes increase offspring swimming speed, whereas when the gametes combine of warm-exposed matched parents an antagonistic interaction occurs.

The lack of change in offspring swimming speed when both parents were exposed to warming may be due to the energetic costs of maximal prolonged swimming. While a higher critical swimming speed might increase predator evasion or allow feeding in strong currents and understandably be favoured by selection (Plaut, 2001), it may come at a greater energetic cost and trade off with other important traits. For example, sablefish exhibiting faster (compensating) growth after a period of reduced growth had a lower critical swimming speed than non-compensating fish (Sogard & Olla, 2002). In other words, when both mothers and fathers are exposed to warming, they produce offspring with a similar swimming speed to control fish because that speed may be optimal for the energy budget of the whole animal. Therefore, faster swimming in offspring of independently exposed mothers and fathers may be maladaptive, or at least could have consequences for other fitness related traits (Arnold, Nicotra, & Kruuk, 2019). This is not surprising given there is weak evidence across taxa for adaptive transgenerational plasticity (Sánchez-Tójar et al., 2020; Uller et al., 2013). The ability to achieve a higher maximum sustained swimming speed, as measured in this study, may be beneficial under some circumstances (e.g. continuous swimming in a high current environment), but could come at the expense of energy expenditure on other traits, such as growth or storage. Though I did not find evidence of a trade-off in offspring body size or condition from independently exposed mothers and fathers (see Chapter 4).

Increased swimming speed was mostly observed when offspring were reared in present-day temperature from mothers or fathers independently exposed to warming. When offspring of warm-exposed mothers or fathers were reared in +0.75°C or +1.5°C, swimming speeds were generally similar to offspring with both parents developed in current-day control temperature in the respective offspring rearing and swimming temperatures. This interactive pattern suggests transgenerational plasticity and fits theoretical expectations of multigenerational environmental variability (Burgess & Marshall, 2014). The greatest legacy of parental effects occurred in offspring of warm-exposed mothers or fathers reared in present-day conditions possibly due to the lack of change in environmental conditions from mature parent to offspring (i.e. parents

reproduced in present-day control temperature). However, for offspring reared in +0.75°C or +1.5°C the shift in environmental conditions potentially cued juveniles to respond developmentally to this altered environment and maintain their critical swimming speed. Favouring within-generation plasticity when parental conditions do not effectively predict offspring conditions, is again expected from theory (Uller, 2008). For instance, within-generation plasticity to elevated temperature significantly overrode transgenerational plasticity of body size in stickleback fish (*Gasterosteus aculeatus;* Shama, 2017) and across a wide range of morphological and physiological traits in *Drosophila melanogaster* (Crill, Huey, & Gilchrist, 1996). Despite this, maternal influence was greater than paternal since offspring of warm mothers mismatched with control fathers also swam faster when reared in +1.5°C and swum at 28.5°C. This is likely owing to the increased opportunities for non-genetic transfer of information by mothers compared with fathers (Mousseau & Fox, 1998). The general finding of faster swimming offspring from thermally mismatched parents dissipating with juvenile developmental cues supports the perspective that faster critical swimming is not adaptive.

My results show that transgenerational plasticity occurs through both maternal and paternal germ lines, and interestingly swimming speed increased only when mothers and fathers were independently exposed to warming. By contrast, when both parents were exposed to warming their offspring had a similar swimming speed to control parents, which may suggest a transgenerational response to maintain a swimming speed that is optimal for the energy budget of the whole animal. Faster swimming speed is usually considered adaptive, but higher sustained swimming speed will likely have implications for other energy dependent activities, such as growth, storage and maintenance. Indeed, if higher sustained swimming speed is adaptive at higher temperature and considering *A. polyacanthus* is morphologically identical and monogamous with biparental care, we would expect our results to conform to the additive model, where offspring from warm mothers and fathers had the combined effects of independently exposed mothers and fathers on swimming performance. The absence of an additive effect, and overriding influence of developmental conditions for offspring from mismatched parents, suggests that thermally mismatched mothers and fathers could produce offspring reared in present-day conditions that are not optimally suited to swimming in warmer water. My study highlights the importance of considering maternal, paternal, and biparental contributions as my results would have been masked if I had combined cues coming from mothers and fathers (i.e. compared offspring of two warm-exposed parents to control parents). It also stresses the importance of placing offspring in a range of relevant environments to estimate within-generation and transgenerational plasticity. Whether the transgenerational

plasticity observed in this study is adaptive, or not, deserves further investigation as it may influence the population's ability to adjust to rapid ocean warming.

Chapter 6 General Discussion

Although studied for decades from an evolutionary perspective, phenotypic plasticity has recently become a topic of more applied interest because of its potential to be a lifeline for organisms in a rapidly changing climate. However, phenotypic plasticity may depend on the sex of the individual or timing and duration of environmental exposure (Angilletta Jr, 2009; Donelson et al., 2018; West-Eberhard, 2003). Plasticity in one generation may also interact with environmental conditions experienced in future generations (Salinas et al., 2013). Further, not all plastic changes are adaptive, as the machinery for plasticity may entail costs and the benefits of plasticity in one trait may trade-off with another (Auld et al., 2010; DeWitt et al., 1998; Murren et al., 2015; Schuler & Orrock, 2012; Stearns, 1989b). Given these potential limitations, unexpected ecological outcomes of phenotypic plasticity and complex interactions between generations seem likely. Yet few studies to date have considered these complexities in a climate change context.

This thesis used a robust experimental design to unravel how sex and exposure timing within and between generations influences a coral reef fish's ability to persist in a warming ocean. I found that solely developmental exposure of *A. polyacanthus* to warming generally improved performance later in life (Chapters 2, 3, 4, 5). This was especially true for females and these benefits seemed to be passed to offspring (Chapters 3 and 4). However, the longer either sex were exposed to warming the greater the impact on reproductive performance and newly hatched offspring quality. If warming continued from development to maturity, females did not breed irrespective of their partner's thermal experience, which could have devastating consequences on future population sustainability (Chapter 3). Males continuously exposed to warming paired with females reared in present-day temperature, were able to reproduce but produced fewer and lower quality offspring (Chapter 3). Furthermore, offspring at three months post hatching from any parent exposed to warming were lighter and lower in condition (Chapter 4), which may be the result of an increased metabolic rate (Munday et al., 2016). Interestingly, non-adaptive changes in offspring swimming performance seemed to occur when only one parent developed in elevated temperature (Chapter 5). This was reversed when both parents developed in elevated temperature and may indicate that biparental exposure to warming is required to maintain what may be an optimal swimming speed for the energy budget of the whole animal (Chapter 5). My research shows the complexity of predicting the effects of ocean warming on tropical fish populations, since the duration, ontogenetic timing, and sex-linked experiences to warming interact, within and between generations.

6.1 Ontogenetic timing and duration of warming

Exposure to warming in either the developmental or reproductive life-stage induced phenotypic change within and across generations. Developmental plasticity allowed *A. polyacanthus* to swim faster and further and be in better physical condition in elevated temperatures compared to siblings reared in present-day temperature (Chapters 2, 4, 5). This supports previous studies on *A. polyacanthus* and other reef fishes that exposure to warming during development can be beneficial (Donelson, 2015; Donelson et al., 2011; Green & Fisher, 2004; Grenchik et al., 2013; Jarrold & Munday, 2018). Pairs exposed to elevated temperature during development or reproduction bred in similar proportions to pairs reared in present-day temperature, suggesting the ontogenetic timing of exposure may not have an impact on breeding probability for this species (Chapter 3). However, there was a positive interaction with sex, such that when only females developed in higher temperature they bred slightly more (Chapter 3). In fact, maternal developmental exposure to warming resulted in greater provisioned offspring at hatching, which then grew to be slightly longer, heavier, and in better physical condition at three months post hatching compared to other parental combinations exposed to warming (Chapters 3 and 4). Possibly these offspring had a head start. By contrast, solely reproductive exposure to warming resulted in purely negative effects within and between generations. These pairs produced fewer clutches, faster developing embryos, shorter hatchlings, and shorter, lighter, and lower condition offspring at three months post hatching in all rearing temperatures compared to pairs reared in present-day temperature (Chapters 3 and 4). Therefore, the developmental life-stage appears to provide the greatest opportunity for adaptive plasticity within and between generations in this species. These findings also corroborate previous reviews and meta-analyses that early life experiences in the parental generation, particularly by mothers, seem to result in adaptive plastic changes in offspring (Burton & Metcalfe, 2014; Radersma et al., 2018; Sánchez-Tójar et al., 2020; Yin et al., 2019). Furthermore, interactions with sex were sometimes present, highlighting the importance of considering both the ontogenetic timing and sex in future experimental work on plasticity.

Developmental exposure to warming induced beneficial plasticity but this depended on the duration of exposure with potential trade-offs the longer exposed. Exposure of *A. polyacanthus* to elevated temperature for 3 or 7 dph was insufficient to produce a phenotypic response but one and three months exposure post hatching resulted in an enhanced escape performance (Chapter 2), which matched with previously estimated thermosensitive periods (Donelson et al., 2011; Rodgers et al., 2017). Since phenotypic change can be energetically costly, responding to incorrect cues could be maladaptive, thus it is likely that a certain duration of cue

exposure is required before a permanent phenotypic change is induced (Angilletta Jr, 2009; Bonamour, Chevin, Charmantier, & Teplitsky, 2019). Three months exposure to elevated temperature post hatching, however, resulted in trade-offs with reduced body weight and length (Chapter 2). Smaller size can be an adaptive response to increased heat tolerance in water breathers (Forster et al., 2012; Leiva et al., 2019) but that was not the case here (Chapter 2). Smaller size can also increase the risk of predation and reduce competitive ability (Goatley & Bellwood, 2016; Meekan et al., 2006; Sogard, 1997). Interestingly, physical condition improved slightly in these juveniles (Fulton's K condition factor increased by 3%, on average, in juveniles exposed to +2°C for 3 months post hatching compared to all other treatments). In Chapter 3, I observed a reduction in body length and maintenance of weight, which allowed physical condition to improve when offspring were reared in elevated temperature for three months post hatching compared to present-day reared siblings. The maintenance of weight in Chapter 3 and not Chapter 2 may be due to a slightly higher food level in that experiment (0.5% approx. increase) and a lower elevated temperature treatment (+0.75-1.5°C instead of +2°C). Nevertheless, these findings suggest high condition is important under longer durations of exposure to elevated temperature, whether that means adjusting standard length or weight to achieve it. Further, this may mean that the reduction in body size with three months exposure to warming post hatching may not be a disadvantage after all. In summary, sufficient time is required to induce developmental plasticity to elevated temperature, likely to prevent incorrect responses to the environment. As exposure duration increases within development there may be trade-offs with other traits and/or further benefits, emphasising the need for future studies to consider a whole organism approach (rather than a single trait approach; Forsman, 2015).

When exposure to warming continued into maturity, however, the outcome was catastrophic. No pairs bred when they were exposed to elevated temperature during both developmental and reproductive life-stages and since a similar result was observed when only females were continuously exposed, this suggests that females were the limiting factor (Chapter 3). It is interesting that for *A. polyacanthus* females, developmental exposure to elevated temperature alone slightly increased the likelihood of breeding yet a longer duration greatly reduced it (Chapter 3). Similar findings were observed in female seed beetles (*Stator limbatus*; Stillwell & Fox, 2005). A pertinent question is whether the effects of elevated temperature on breeding extend throughout life or was reproduction delayed? When the timing treatments were continued into the second breeding season, pairs of males and females exposed continuously to elevated temperature bred but in lower proportions than the other treatments. This suggests that although females struggled to breed during the first breeding season (~2 years of age), after

sufficient time some females were able to bred in the second breeding season (~3 years of age). Delayed breeding can increase the risk of mortality before that individual contributes to the next generation and lower lifetime reproductive output (Newton, 1985), but could be a strategy to increase lifetime fitness if environmental conditions fluctuate (Koons, Metcalf, & Tuljapurkar, 2008). Males exposed during both developmental and reproductive life-stages, on the other hand, bred in similar proportions to present-day reared fish but their embryos and hatchlings were the smallest compared to other treatments' progeny (Chapter 3). Further, their offspring at three months post hatching were lighter and in lower condition than offspring from parents reared in present-day conditions, however, they were generally similar to the treatments where males only developed in elevated temperature or pairs solely reproduced in elevated temperature (Chapter 4). Therefore, while extended paternal exposure to warming may negatively affect embryos and newly hatched offspring this does not appear to have an additive effect on juveniles, at least in regards to body size and physical condition (Chapters 3 and 4). This underscores why phenotypic plasticity within and between generations must be considered, since what may be evident in one generation may not be so in the next.

6.2 Sex-linked plasticity

Elevated developmental temperature affected male and female reproductive capacity differently and these had flow on effects to offspring performance. Females exposed to warming solely in development bred more, laid larger eggs, and provided greater provisioning to their hatchlings compared to males exposed to warming solely in development or pairs reared in present-day temperature (Chapter 3). Offspring from these mothers were slightly lighter and in lower condition by three months post hatching compared to progeny from present-day reared pairs, yet the decrease wasn't as large and length was not affected compared to offspring from fathers exposed to warming in development (Chapter 4). It's possible the larger eggs and extra yolk allowed these offspring to attain a greater size and stay in better condition than offspring from fathers exposed to warming in development (Bagenal, 1969; Brooks et al., 1997; Fox, 1994). While these findings may suggest the mother's developmental environment is a good predictor of the offspring environment (and thus anticipatory maternal effects may be selected for), this is unlikely since there was actually a trend of offspring weight and condition worsening when siblings were reared in the same elevated temperture as their mother (Chapter 4; Lind et al., 2020; Marshall & Uller, 2007). Instead these are likely carry-over maternal effects. By contrast, pairs consisting of males exposed to elevated temperture solely in development bred in similar proportions to present-day reared pairs but they produced fewer clutches and embryos took

longer to develop (Chapter 3). These males may be less likely to engage with their female, potentially due to stress, and thus a second clutch is not produced (Hilder & Pankhurst, 2003). Reduced copulation along with smaller testes and sperm were observed in male beetles (*Callosobruchus maculatus*) and moths (*Plodia interpunctella*) exposed to elevated temperture during development only (Iossa et al., 2019; Vasudeva, Deeming, & Eady, 2014, 2018). Poor quality sperm induced by a stressful environment has been shown to result in smaller offspring and that could be an explanation as to why offspring from fathers exposed to elevated temperture solely in development were the smallest at three months post hatching compared to offspring from other parental treatments, including parents reared in present-day temperature (Chapter 4). This along with previous evidence suggests a potential epigenetic mechanism (Ryu, Veilleux, Donelson, Munday, & Ravasi, 2018; Veilleux et al., 2015), which I hope molecular investigation in progress from this experiment will shine a light on. Lastly, I found sons and daughters were similarly affected by their parents' thermal environment (Chapter 5). My findings highlight how males and females differ in their response to elevated temperature and how this translates to phenotypic changes in the next generation.

Instead of sex-specific parental effects per se, the swimming performance of offspring depended on whether parents were thermally matched or mismatched during development. Offspring of mothers or fathers independently exposed to warming in development swam faster than juveniles where both parents developed in present-day temperature, or where both parents developed in warm conditions (Chapter 5). In nature, faster critical swimming speed may enhance a juvenile's ability to escape predators or feed in a current, but could also come at an energetic cost (Plaut, 2001; Sogard & Olla, 2002). Offspring of mothers and fathers exposed to warming in development maintained a swimming speed that may be optimal for the energy budget of the whole animal. Therefore, the increase in swimming speed in offspring from thermally mismatched parents could be a maladaptive parental effect (specifically transgenerational plasticity/anticipatory parental effects owing to an interaction between parent and offspring environments). Similar maladaptive parental effects were observed when threespine stickleback (*Gasterosteus aculeatus*) mothers or fathers were independently exposed to predators (Lehto & Tinghitella, 2020). These results highlight the importance of considering maternal and paternal non-genetic contributions since they would have been masked if only biparental exposure was studied. They also draw attention to the complex and potentially non-adaptive ways transgenerational plasticity may be induced in response to warming.

6.3 Family-level effects

Family-level effects were minimal compared to the influence of the parent or offspring's environment (Chapters 2, 3, 4, 5). This confirms that the previously discussed phenotypic variation is indeed due to phenotypic plasticity and not differential performance among genotypes (Donelson et al., 2018). This might be interpreted as indicating low genetic variation in the traits I measured, which may mean there is limited capacity for *A. polyacanthus* to genetically adapt in higher temperatures. However, the number of breeding pairs used to start my experiments were insufficient to reach such a conclusion. Low genetic variation is not surprising in fitness related traits like reproduction, because strong selection on such traits will erode genetic variance through time (Fisher, 1930; Mcfarlane et al., 2014; Teplitsky et al., 2009). Indeed, Salles et al. (2020) recently demonstrated very low genetic variance in lifetime reproductive success in a wild clownfish (*Amphiprion percula*) population. By contrast, substantial additive genetic variance in metabolic traits across temperatures was previously demonstrated in *A. polyacanthus* from the same region of the Great Barrier Reef (Munday et al., 2016). Munday et al. (2016) also showed significant additive genetic variance in body weight when *A. polyacanthus* were three months post hatching. This suggests that reproductive and metabolic traits exhibit different magnitudes of genetic variance to warming and/or larger samples sizes than what was used in my studies on phenotypic plasticity are needed to detect genetic variance in these traits.

6.4 Phenotypic plasticity: mechanisms and evolution

Whether plasticity was induced and had a positive or negative outcome depended on the ontogenetic timing and duration of exposure to warming, in addition to sex (Chapters 2, 3, 4, 5). Previous studies that have considered either all or some of these circumstances within a climate change context (Donelson et al., 2016; Fuxjäger et al., 2019; Salinas & Munch, 2012; Schwanz, Crawford-Ash, & Gale, 2020; Shama et al., 2016, 2014; Shama & Wegner, 2014) or in other novel environments show similar complex patterns (Crill et al., 1996; Hellmann, Bukhari, et al., 2020; Hellmann, Carlson, & Bell, 2020; Jensen et al., 2014; Lehto & Tinghitella, 2020; Pembrey et al., 2006; Radersma et al., 2018; Stillwell & Fox, 2005). This may suggest plastic changes within an organism have a multitude of underlying non-genetic mechanisms. Wang et al. (2016) show that hypoxia exposure triggers epigenetic changes in the methylome of sperm and alters the expression of genes and proteins related to spermatogenesis and gene silencing, resulting in fewer and slower sperm within and between generations. Alternatively, maternal adult diet can influence the amount of essential fatty acids in embryos, which have consequences for offspring

fitness (Fuiman & Perez, 2015). These are just a few examples of possible mechanisms (see Bonduriansky & Day, 2009; Ho & Burggren, 2010). While epigenetic changes such as DNA methylation are likely an important driver of the phenotypic plasticity observed in *A. polyacanthus* (Ryu et al., 2018, 2020; Veilleux et al., 2015), further investigation is currently underway. Despite the logistical challenges, future studies could aim to measure phenotypic, molecular, hormonal, and metabolic changes within and between generations to improve understanding of the underling mechanisms of phenotypic plasticity.

Phenotypic plasticity is often viewed as way that organisms will be able to cope with climate change (i.e. it is beneficial). However, a number of the plastic responses observed in my thesis appear maladaptive. While I did not directly measure fitness, many of the traits I measured can be linked to fitness based on previous research. In some circumstances, phenotypic change in one trait may trade-off with another, such as reduced offspring weight and condition at three months post hatching from warm-exposed parents likely being due to beneficial changes to metabolic rates (Chapter 4; Munday et al., 2016). Alternately, increasingly unreliable environmental cues with climate change may increase maladaptive plasticity (i.e. evolutionary traps; Donelan et al., 2020; Sheriff, Dantzer, Love, & Orrock, 2018; Van Dyck, Bonte, Puls, Gotthard, & Maes, 2015). This is because maladaptive plasticity is predicted to occur when the environment is incorrectly anticipated and the phenotype is poorly matched (Auld et al., 2010). My results fit with the increasingly common theme in the literature that parental effects often appear non-adaptive (Nilsson et al., 2018; O'Dea, Noble, Johnson, Hesselson, & Nakagawa, 2016; Radersma et al., 2018; Sánchez-Tójar et al., 2020; Uller et al., 2013). Though there are recent exceptions to this, including in *A. polyacanthus* (Donelson & Munday, 2015; Donelson, Munday, McCormick, et al., 2012; Tariel et al., 2020; Yin et al., 2019). Interestingly, O'Dea et al. (2016) argues that maladaptive plasticity may prove beneficial over a longer time period owing to increased phenotypic variation. Moreover, maladaptive plasticity may itself facilitate adaptive evolution (O'Dea et al., 2016). For instance, the direction of plasticity in gene expression was generally opposite to the direction of adaptive evolution, suggesting that adaptive plasticity may constrain evolution, while maladaptive plasticity potentiates evolution by increasing the strength of directional selection (Ghalambor et al., 2015). This underscores the importance of experiments that extend for several generations, albeit time-consuming in organisms with long generations times like *A. polyacanthus* (e.g. 2 years), it is a necessary step to understand the interface between plasticity and evolution.

6.5 Importance of realistic simulations of nature

Diurnal temperature variation may be one possible explanation as to why the effects of warming were accentuated in my thesis compared to previous studies using constant daily temperatures. Previous findings suggest that *A. polyacanthus* from the same region of the Great Barrier Reef can restore their reproductive capacity to control levels with constant +1.5°C for one generation (Donelson et al., 2014). By contrast, I observed disrupted breeding in pairs of males and females exposed during developmental and reproductive life-stages to +1.5°C with a daily variation, which instead matches previous results for *A. polyacanthus* reared at a constant +3°C (Chapter 3; Donelson et al., 2014, 2010, 2016). When parents were exposed to warming with diurnal variation, offspring weight and physical condition at three months post hatching were greatly reduced, whereas previous studies in constant elevated temperatures did not observe such significant effects in the first months post hatching (Chapter 4; Donelson et al., 2014; Donelson, Munday, & McCormick, 2012). This could mean more dramatic effects to reproduction and offspring performance may occur in natural settings at a lower increase than constant temperature experiments suggest, although further investigations are required to confirm this in *A. polyacanthus*. In mosquitoes, exposure to daily temperature variation resulted in greater suffering compared to individuals exposed to constant elevated temperature (Paaijmans et al., 2013). This is not surprising given that Vasseur et al. (2014) have shown that temperature variation poses a greater threat to ectotherms than an average increase in temperature, highlighting that climate change is best understood by considering changes in the mean and variance of temperature concurrently. Jensen's inequality (a mathematical property of nonlinear functions) further supports that the response of an organism to average temperature is different than the organism's average response to variable temperature (Kroeker et al., 2020; Ruel & Ayres, 1999). Therefore, when organisms exist near their thermal limits as coral reef fishes often do (McLeod et al., 2014; Rummer et al., 2014), Jensen's inequality predicts an exacerbation of the effects of warming (Kroeker et al., 2020). What's even more interesting is that Donelson et al. (2014, 2012) incorporated seasonal temperature variation (but not diurnal), which potentially suggests small differences in simulating variation may have significant effects on the outcome. Future experiments should attempt to approximate nature's variation to accurately estimate the effects of climate change on organisms (Burggren, 2018).

6.6 Will plasticity help organisms persist in a changing climate?

My findings suggest simulated heatwaves and average warming can induce phenotypic plasticity in a coral reef fish and may be adaptive, but this is dependent on when the exposure occurred,

for how long, the sex of the individual exposed, and the trait of interest. From a whole organism perspective, elevated temperature and associated plastic changes seem maladaptive given that female *A. polyacanthus* struggle to bred when exposed to average warming. By contrast, a similar study found within and between generation plasticity to ocean warming in threespine stickleback fishes (*Gasterosteus aculeatus*) mostly beneficial, but again it depended on exposure timing and sex (Fuxjäger et al., 2019; Shama et al., 2016, 2014; Shama & Wegner, 2014). Yet for tropical ectotherms, which live life on the thermal edge, the overall outcome is more likely to be negative. Although no other topical ectotherm has been studied as intensely as *A. polyacanthus* (except possibly guppies e.g. Le Roy, Loughland, & Seebacher, 2017), a multigenerational experiment on warming and ocean acidification in a tropical sea urchin showed likewise mostly negative effects (Uthicke et al., 2021). More rigorous experiments are needed in other species, especially from the tropics, to understand the generality of my findings.

To truly understand how climate change affects organisms and whether plasticity may help them cope, multi-stressor experiments are needed. Concurrent elevated CO_2 and temperature and/or hypoxia are some of the better studied multi-stressor examples (Bernhard et al., 2021; Harvey, Gwynn-Jones, & Moore, 2013; Jarrold & Munday, 2018; Miller et al., 2015; Przeslawski, Byrne, & Mellin, 2015; Suckling et al., 2015). However, such experiments rarely consider how these stressors will covary at temporal scales (Gunderson, Armstrong, & Stillman, 2016). Reum et al. (2016) has suggested experimental designs to incorporate these complexities and provided real-world data on the covaraince of acidification, temperature, and oxygen in coastal upwelling systems. Furthermore, there are relatively few multi-stressor experiments that span multiple generations. One such example exposed a marine polychaete (*Ophryotrocha labronica*) to warming or the combination of warming and increased salinity across two generations (Jarrold et al., 2019). The authors also measured how the timing of exposure (embryos vs juveniles) influenced developmental plasticity, finding that plastic changes were only observed in the multi-stressor treatment and trade-offs occurred based on the timing of exposure. Across generations, temperature alone had several positive effects on offspring performance, however, combined with increased salinity most of these positive effects disappeared (Jarrold et al., 2019). This means single stressor experiments could overestimate adaptive parental effects in this system. More broadly, multi-stressor interactions can be complex (Cote, Darling, & Brown, 2016; Crain, Kroeker, & Halpern, 2008) and coupled with my multifaceted findings in this thesis provide challenging but exciting opportunities for future research. Experiments that span multiple generations and include multiple stressors, while

difficult, are needed to provide a complete picture of climate change effects on organisms and their ability to adjust with phenotypic plasticity.

6.7 Concluding remarks

This thesis demonstrates that thermal experiences based on the timing, duration, and sex within and between generations can result in diverse phenotypic outcomes. While developmental exposure to warming may be beneficial, particularly for females and their offspring, I also observed costs of plasticity, trade-offs among traits, and unexpected maladaptive responses within and between generations. Thus, in order to fully understand the implications of climate change and the ability of organisms to cope through phenotypic plasticity, it will be useful to design future experiments that span multiple generations and measure how the timing and duration of exposure to future climate scenarios, in addition to the sex of the organism, influences performance. Furthermore, since my results suggest environmental variation may exacerbate the effects of warming, it is important that the next generation of experiments strive to simulate nature closely to accurately predict future responses of organisms. Similarly, future studies need to examine the underlying mechanisms of phenotypic plasticity and further explore the interplay with evolution. Further careful experimentation, in a wider variety of species and stressors, will be critical to accurately predict the responses of organisms to climate change and their capacity to adjust through phenotypic plasticity.

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Appendix

Chapter 2

Table 2.1 Priors used in the hierarchical mixed models.

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

Note. The prior distributions are provided in italics and the prior means and standard deviations in brackets. Majority of the standard deviations (also known as scales) were specified via the rstanarm package by multiplying the standard deviation of the dependent variable by 10. NA, not applicable.

Table 2.2 Escape direction coefficients

	Component 1			Component 2		
	Mean	Lower UI	Upper UI	Mean	Lower UI	Upper UI
0 dph (control)	-0.820	-1.213	-0.421	0.187	-0.215	0.588
3 dph at +2°C	0.223	-0.264	0.688	-0.339	-0.851	0.144
7 dph at +2°C	0.016	-0.409	0.485	-0.060	-0.544	0.429
30 dph at +2°C	-0.286	-0.788	0.162	-0.397	-0.871	0.081
108 dph at +2°C	-0.030	-0.484	0.470	-0.535	-1.036	-0.046*
Performance temp. 30.5°C	-0.161	-0.464	0.134	0.059	-0.244	0.376
Orientation						
stim. impact						
cosine	0.981	0.705	1.288*	0.011	-0.269	0.306
sine	0.171	-0.047	0.388	0.662	0.466	0.873*

Note. Bayesian posterior means and 95% highest posterior density uncertainty intervals (UI) of the escape direction in radian for both components of the linear regression coefficients. An asterisk (*) indicates that the UI does not intersect with zero, i.e. strong evidence for an effect.

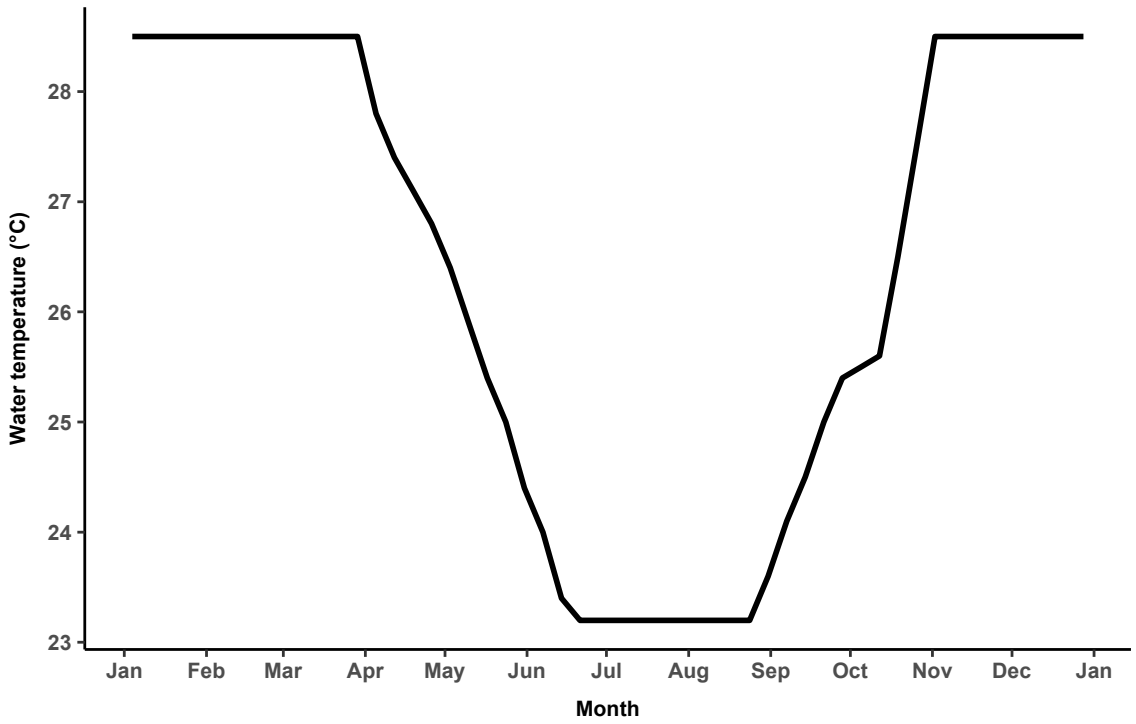


Figure 2.1 Weekly mean water temperature experienced by the wild-caught parents once in captivity. Approximately based on a mid-latitude reef on the Great Barrier Reef (AIMS, 2016).

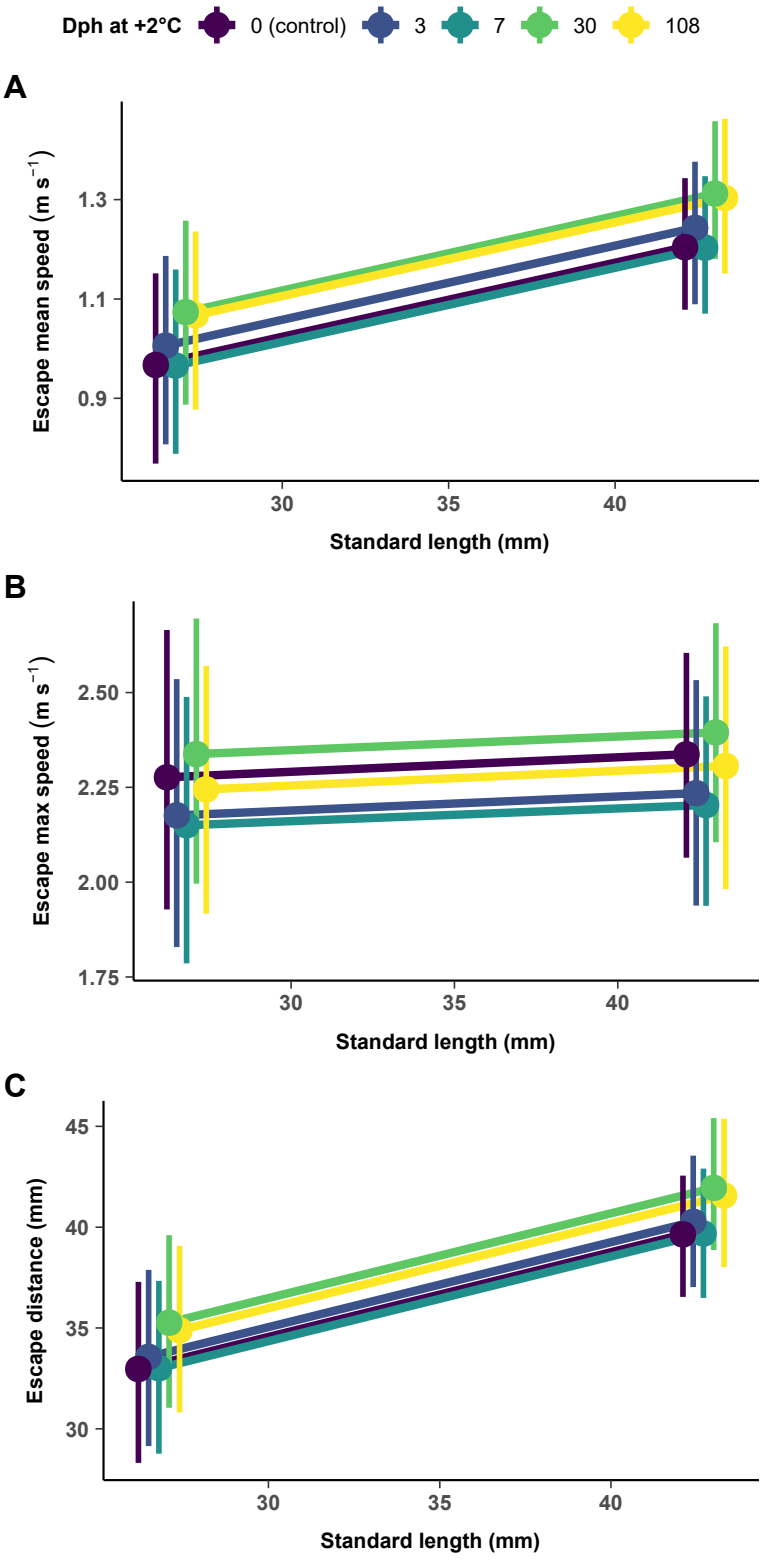


Figure 2.2 Influence of standard length on escape speed and distance. Bayesian posterior median values (circles) with 95% highest posterior density uncertainty intervals (vertical lines) of ***A*** *escape mean speed,* ***B*** *escape maximum speed, and* ***C*** *escape distance in relation to the fish's minimum and maximum standard length, separated by exposure duration treatments. Dph – days' post hatching.*

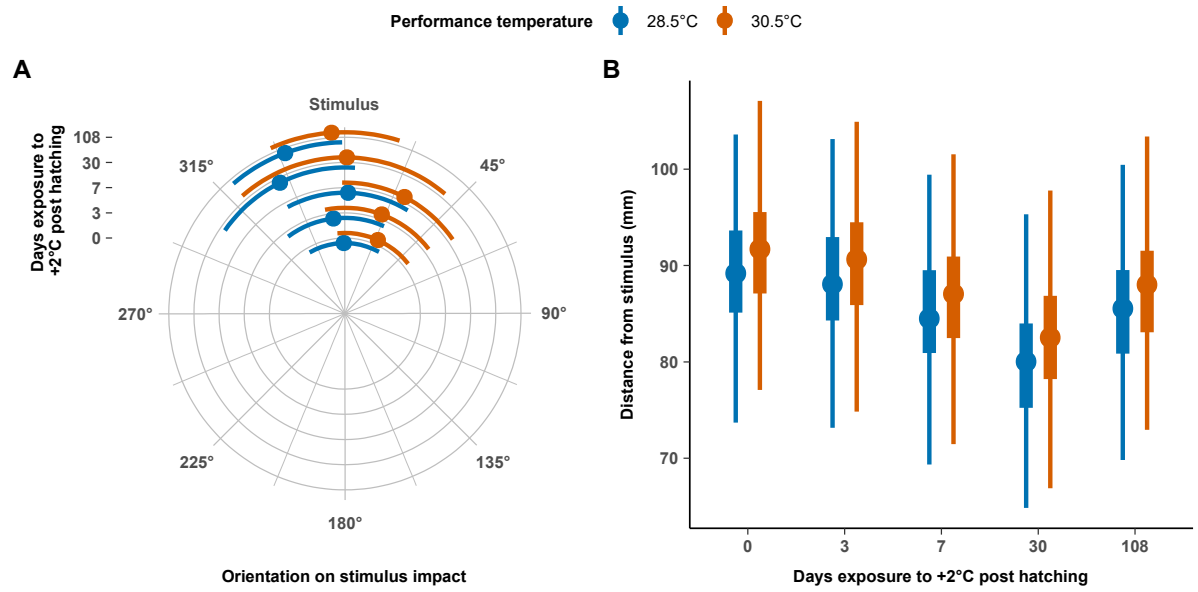


Figure 2.3 Orientation and distance from stimulus on impact in escape performance trials. ***A*** *Bayesian posterior mean values (circles) and 95% highest posterior density uncertainty intervals (thin lines) of the fish's orientation on stimulus impact and* ***B*** *Bayesian posterior median values (circles) and 95% highest posterior density uncertainty intervals (thin lines) and 50% uncertainty intervals (thick lines) of the fish's distance from the stimulus on impact.*

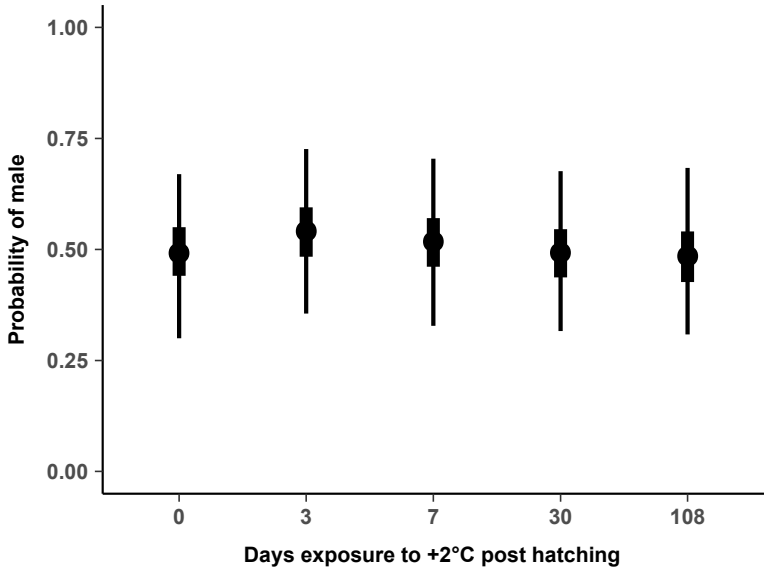


Figure 2.4 Sex ratio. Bayesian posterior median values (circles) with 95% highest posterior density uncertainty intervals (thin lines) and 50% uncertainty intervals (thick lines) of the probability of male sex.

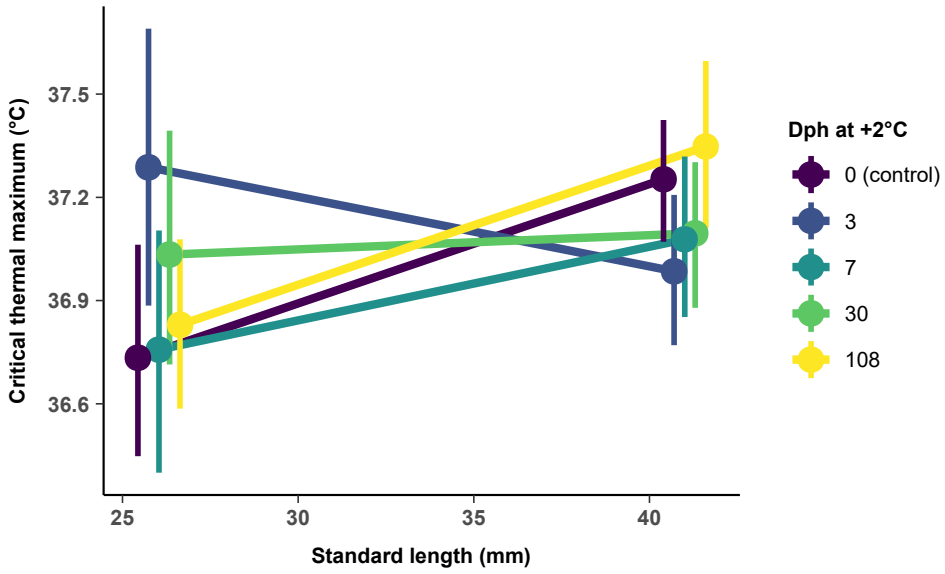


Figure 2.5 Influence of standard length on CT_{max}. Bayesian posterior median values (circles) with 95% highest posterior density uncertainty intervals of the CT_{max} in relation to the fish's minimum and maximum standard length. Dph – days' post hatching.

Chapter 3

Table 3.1 Priors used in each model

Model	*Intercept*	*Slope*	*Error standard deviation*
Breeding probability	*Normal*(0, 20 log odds)	*Normal* (0, 20 log odds)	–
Clutch size	*Normal*(0, 10 log)	*Normal* (0, 2.5 log)	–
Total eggs per pair	*Normal*(0, 10 log)	*Normal* (0, 2.5 log)	–
Egg area	*Normal*(0, 5.12 mm^2)	*Normal* (0, 1.28 mm^2)	*Exponential* (rate 0.51)
Embryonic duration	*Normal*(10, 3 days)	*Normal* (0, 2 days)	*Exponential* (rate 0.72)
Embryonic mortality	*Normal*(0, 10 log odds)	*Normal* (0, 2.5 log odds)	–
Hatch weight	*Normal*(3, 5.64 mg)	*Normal* (0, 1.41 mg)	*Exponential* (rate 0.56)
Hatch standard length	*Normal*(5, 3.21 mm)	*Normal* (0, 0.8 mm)	*Exponential* (rate 0.32)
Hatch yolk area	*Normal*(0, 2.5 mm^2)	*Normal*(0, 0.63 mm^2)	*Exponential* (rate 0.25)

The prior distributions are provided in italics and the prior means and standard deviations in brackets unless otherwise specified. Majority of the standard deviations were acquired by multiplying the standard deviation of the dependent variable by 10 via the rstanarm package.

Table 3.2 Summary statistics

Model Treatment	*n*	Median	50% CI	95% CI	Probability treatment < control	Probability treatment > control
Breeding probability ♂♀🔵	19 pairs	34%	19-41%	5-67%	–	–
♂♀🔵	17 pairs	58%	46-72%	23-91%	15%	85%
♂♀🔵	17 pairs	26%	12-33%	2-60%	64%	36%
♂♀🔵	10 pairs	38%	20-50%	4-79%	44%	56%
♂♀🟠	19 pairs	30%	17-38%	3-64%	57%	43%
♂♀🟠	11 pairs	3%	<0.01-3	<0.01-22%	98%	2%
♂♀🟠	17 pairs	19%	6-22%	1-50%	79%	21%
♂♀🟠	13 pairs	<0.01%	<0.01-<0.01%	<0.01-0.01%	99.98%	0.02%
Clutch size (eggs) ♂♀🔵	7 pairs	327	297-349	247-407	–	–
♂♀🔵	7 pairs	297	273-320	222-370	76%	24%
♂♀🔵	5 pairs	308	278-333	224-404	65%	35%
♂♀🔵	4 pairs	240	217-265	168-316	96%	4%
♂♀🟠	6 pairs	323	295-350	239-418	53%	47%
♂♀🟠	4 pairs	308	274-336	223-423	62%	38%
Total eggs per pair ♂♀🔵	6 pairs	681	567-744	424-995	–	–
♂♀🔵	6 pairs	654	543-720	395-992	57%	43%
♂♀🔵	5 pairs	436	355-479	247-636	96%	4%
♂♀🔵	4 pairs	457	358-496	267-710	94%	6%
♂♀🟠	5 pairs	539	442-594	333-810	84%	16%
♂♀🟠	3 pairs	359	263-391	176-594	97%	3%
Egg area (mm^2) ♂♀🔵	72 eggs	4.25	4.11-4.38	3.82-4.64	–	–
♂♀🔵	70 eggs	4.48	4.35-4.62	4.05-4.94	17%	83%
♂♀🔵	52 eggs	4.15	3.99-4.30	3.67-4.60	67%	33%
♂♀🔵	40 eggs	4.35	4.19-4.53	3.83-4.85	36%	64%
♂♀🟠	55 eggs	4.11	3.96-4.25	3.68-4.55	72%	28%
♂♀🟠	40 eggs	3.76	3.60-3.94	3.24-4.29	96%	4%

Embryonic duration (days) ♂♀🐌	7 clutches	9	9-9	9-10	–	–
♂♀🐌	7 clutches	9	9-9	9-10	57%	43%
♂♀🐌	4 clutches	10	9-10	9-10	11%	89%
♂♀🐌	4 clutches	10	10-10	9-10	4%	96%
♂♀🐌	6 clutches	8	8-8	8-9	99.8%	0.2%
♂♀🐌	4 clutches	8	8-8	8-9	99%	1%
Embryonic mortality ♂♀🐌	2224 eggs	4%	1-5%	0.2-18%	–	–
♂♀🐌	1811 eggs	6%	0.8-6%	0.1-30%	39%	61%
♂♀🐌	1513 eggs	12%	0.9-13%	0.2-52%	19%	81%
♂♀🐌	963 eggs	4%	0.2-5%	<0.01-27%	48%	52%
♂♀🐌	1487 eggs	12%	1-13%	0.1-49%	18%	82%
♂♀🐌	1193 eggs	13%	0.4-13%	0.2-55%	19%	81%
Hatch weight (mg) ♂♀🐌	138 hatchlings	3.3	3.2-3.4	3.0-3.6	–	–
♂♀🐌	160 hatchlings	3.5	3.3-3.6	2.9-3.9	26%	74%
♂♀🐌	80 hatchlings	3.4	3.2-3.6	2.8-3.9	37%	63%
♂♀🐌	80 hatchlings	3.4	3.3-3.7	2.8-4.0	30%	70%
♂♀🐌	120 hatchlings	3.0	2.6-3.0	2.6-3.5	82%	18%
♂♀🐌	58 hatchlings	2.8	2.9-3.2	2.3-3.4	93%	6%
Hatch standard length (mm) ♂♀🐌	138 hatchlings	5.16	5.08- 5.24	4.90-5.40	–	–
♂♀🐌	158 hatchlings	5.14	5.05-5.22	4.88- 5.41	54%	46%
♂♀🐌	80 hatchlings	5.03	4.93-5.12	4.72-5.32	83%	17%
♂♀🐌	78 hatchlings	5.09	5.00-5.20	4.77-5.37	69%	31%
♂♀🐌	120 hatchlings	4.91	4.82-5.00	4.62-5.17	97%	3%
♂♀🐌	58 hatchlings	5.06	4.94-5.15	4.74-5.37	76%	24%
Hatch yolk area (mm^2) ♂♀🐌	138 hatchlings	1.47	1.44-1.49	1.38-1.56	–	–
♂♀🐌	156 hatchlings	1.69	1.64-1.73	1.53-1.84	0.7%	99.3%
♂♀🐌	80 hatchlings	1.54	1.49-1.60	1.37-1.71	21%	79%

♂♀🔵	79 hatchlings	1.71	1.65-1.76	1.53-1.88	1%	99%
♂♀🟠	120 hatchlings	1.44	1.38-1.48	1.28-1.58	67%	33%
♂♀🟠	56 hatchlings	1.56	1.49-1.62	1.37-1.76	17%	83%

Probabilities are expressed as a percent and the closer they are to 0% or 100% suggests greater confidence in a treatment being different relative to the control (♂♀🔵), whereas nearer to 50% suggests less confidence in a treatment being different relative to the control (♂♀🟠). Blue represents the present-day control temperature (in summer 28.5°C with ±0.6°C diurnal variation), orange represents a temperature increase of 1.5°C (in summer 30.0°C with ±0.6°C diurnal variation). The male and female symbols represent the developmental period and the egg and sperm icon represent the reproductive period. CI is Bayesian credible interval (analogous to a Frequentist confidence interval).

Chapter 4

Table 4.1 Priors used in the hierarchical mixed models.

Model	Intercept	Slope	Error standard deviation
Hatch length	*Normal*(5.2, 0.77 mm)	*Normal*(0, [2.25, 1.82, 2.27, 2.05, 2.59] mm)	*Exponential*(rate 3.2)
Hatch weight	*Normal*(3.4, 1.4 mg)	*Normal*(0, [4.16, 3.34, 4.16, 3.79, 4.78] mg)	*Exponential*(rate 1.8)
Hatch yolk area	*Normal*(1.6, 0.61 mm^2)	*Normal*(0, [1.77, 1.44, 1.78, 1.61, 2.06] mm^2)	*Exponential*(rate 4.1)
3mths length	*Normal*(0, 2.5 log)	*Normal*(0, [7.74 5.82 7.77 6.50 8.27 5.30 5.31 2.50 2.50 12.92 9.08 13.21 10.38 13.47 12.48 9.33 12.78 10.48 14.29] log)	*Exponential*(rate 1)
3mths weight	*Normal*(0, 2.5 log)	*Normal*(0, [7.74 5.82 7.75 6.50 8.28 5.30 5.31 2.50 2.50 12.91 9.08 13.20 10.38 13.52 12.47 9.34 12.73 10.47 14.28] log)	*Exponential*(rate 1)
3mths Fulton's K	*Normal*(0, 2.5 log)	*Normal*(0, [7.73 5.82 7.76 6.50 8.28 5.30 5.31 2.50 2.50 12.91 9.07 13.20 10.37 13.51 12.47 9.34 12.77 10.47 14.27] log)	*Exponential*(rate 1)
Sex ratio	*Normal*(0, 10 log odds)	*Normal*(0, 2.5 log odds)	NA

rstanarm v. 2.21.1 default weakly informative priors. The prior distributions are provided in italics and the prior means and standard deviations in round brackets unless otherwise specified. The prior slope provides a standard deviation for each coefficient in square brackets. NA not applicable.

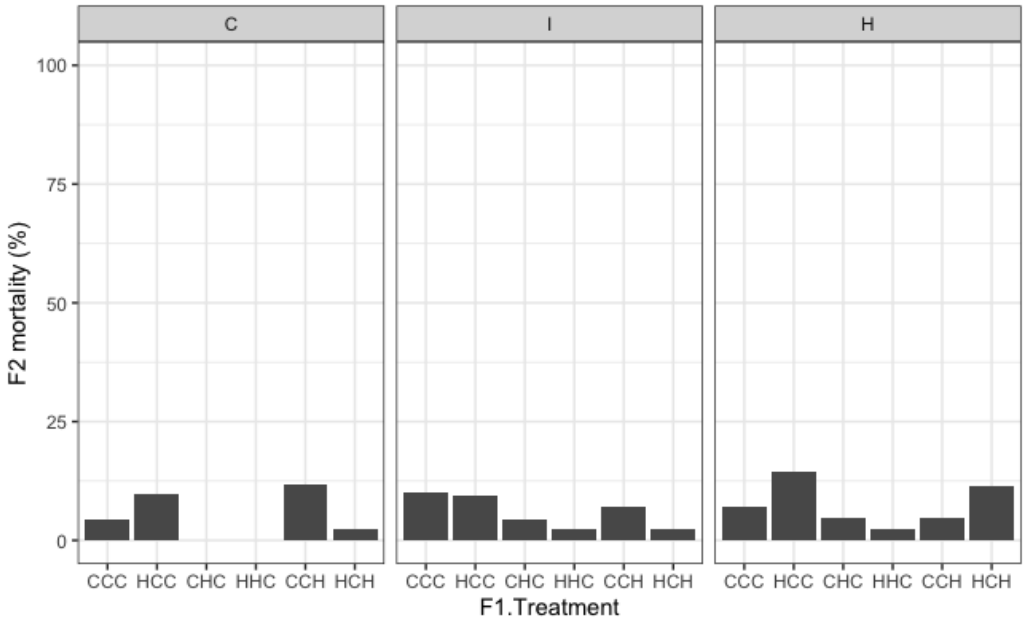
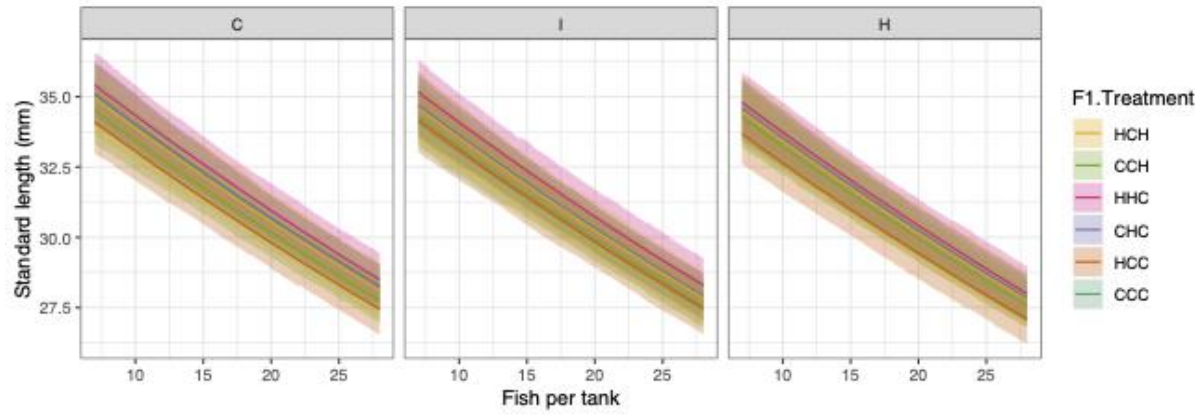
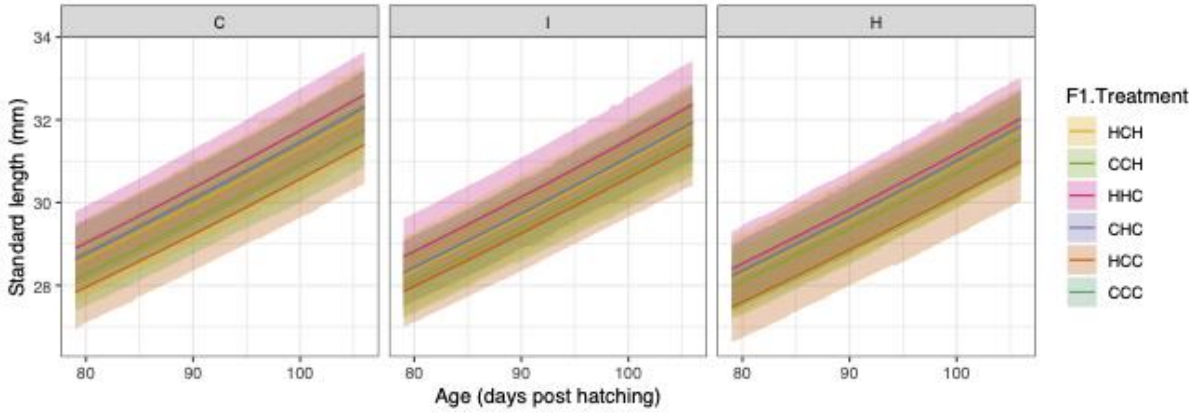


Figure 4.1 Natural mortality of the F2 generation. The parental (Fl) treatment codes are C = control temperature and H = +1.5°C with the first letter indicating the father's developmental temperature, the 2nd letter the mother's developmental temperature, and the third letter the pairs reproductive temperature. The offspring (F2) treatments are denoted by the banners with C = control temperature, I = +0.75°C, and H = +1.5°C.

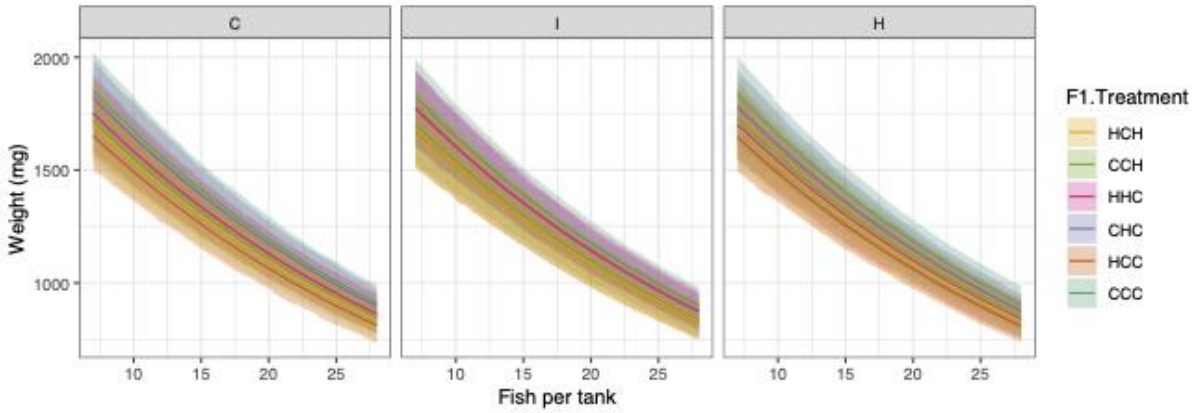
A



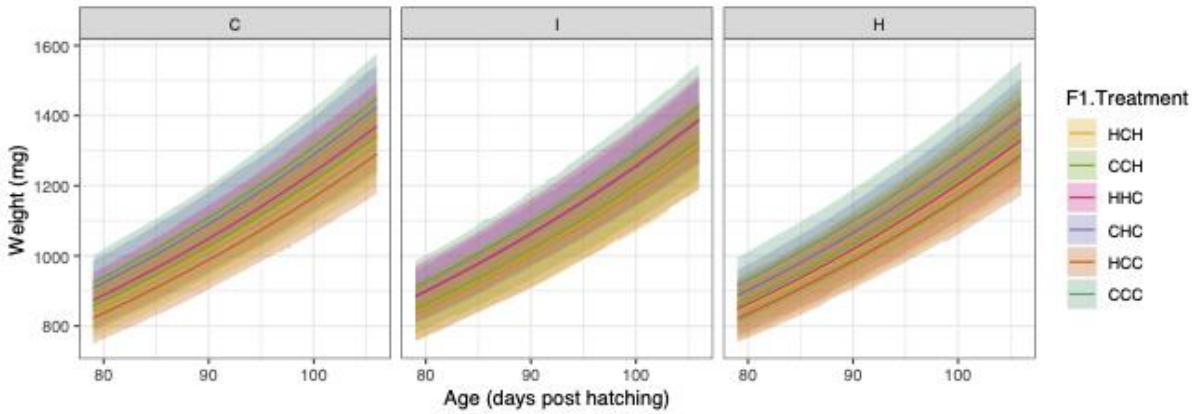
B


C
I
H
Standard length (mm)
34
32
30
28
80
90
100
Age (days post hatching)
F1.Treatment
HCH
CCH
HHC
CHC
HCC
CCC

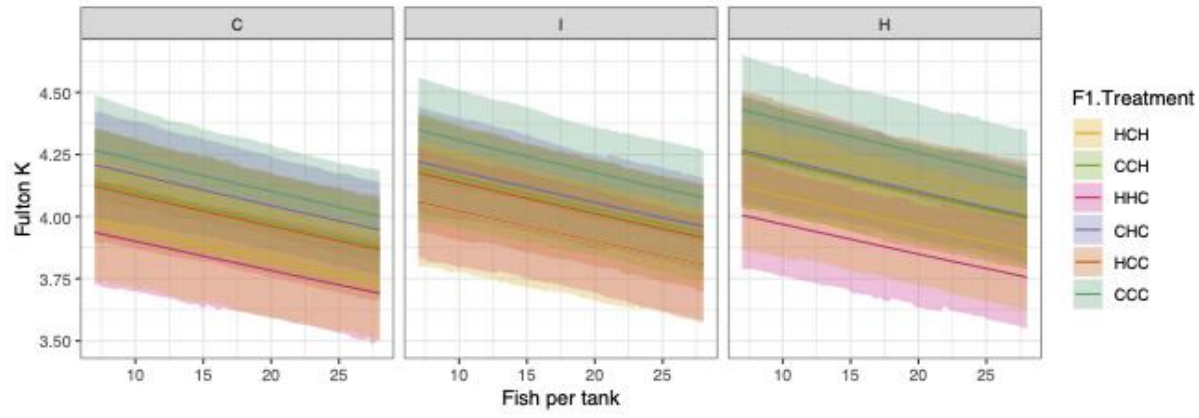
C


C
I
H
Weight (mg)
2000
1500
1000
10
15
20
25
Fish per tank
F1.Treatment
HCH
CCH
HHC
CHC
HCC
CCC

D


C
I
H
Weight (mg)
1600
1400
1200
1000
800
80
90
100
Age (days post hatching)
F1.Treatment
HCH
CCH
HHC
CHC
HCC
CCC

E



F

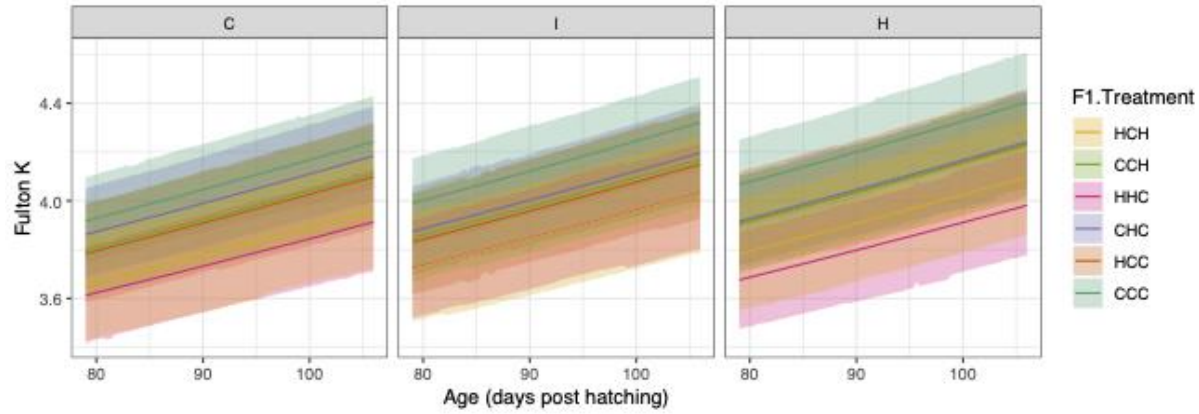


Figure 4.2. Size and condition relationship with fish density and age. Bayesian posterior relationships (solid lines) with 95% credible intervals (ribbons) between offspring A) standard length and density, B) standard length and age, C) weight and density, D) weight and age, E) Fulton's K condition factor and density, and F) Fulton's K condition factor and age, across the parental and offspring temperatures. The parental (F1) treatments are listed to the right of each plot with C = control temperature and H = +1.5°C and the first letter indicating the father's developmental temperature, the 2nd letter the mother's developmental temperature, and the third letter the pairs reproductive temperature. The offspring treatments are denoted by the banners with C = control temperature, I = +0.75°C, and H = +1.5°C.

Chapter 5

Table 5.1 Bayesian priors of final model

I used rstanarm v. 2.21.1 default weakly informative priors. The prior distributions are provided in italics and the prior means and standard deviations in round brackets unless otherwise specified. The prior slope provides a standard deviation for each coefficient in square brackets.

Intercept	*Normal*(8.31, 2.71 bl s^{-1})
Slope	*Normal*(0, [6.23, 7.13, 6.66, 5.76, 5.72, 6.09, 5.67, 2.72, 9.77, 11.72, 10.63, 9.77, 10.89, 10.51, 10.06, 17.43, 11.39, 9.50, 10.27, 10.45, 9.03, 9.54, 8.44, 8.08, 16.33, 30.48, 18.42, 17.13, 28.93, 20.06, 16.59, 17.43, 17.74, 15.43, 16.09, 16.85] bl s^{-1})
Error standard deviation	*Exponential*(rate 0.92)

These priors are technically data-dependent since the standard deviations are based on the scales of the independent variables however because they are reasonably wide the amount of information used is minimal.

Table 5.2 Summary statistics of critical swimming speed in bl s^{-1} at the average fish size of 0.41 g cm^{-1}.

F1 temp.	F2 temp.	Swimming temp.	*n*	Median	50% CI	90% CI
♂♀	control	28.5°C	48	7.85	7.69-7.98	7.52-8.22
		29.25°C	37	8.07	7.92-8.24	7.68-8.47
		30°C	41	8.46	8.29-8.61	8.09-8.86
	+0.75°C	28.5°C	46	8.21	8.03-8.34	7.83-8.60
		29.25°C	47	7.92	7.73-8.07	7.50-8.33
		30°C	46	8.36	8.21-8.55	7.93-8.77
	+1.5°C	28.5°C	48	8.02	7.85-8.16	7.67-8.41
		29.25°C	40	8.15	7.99-8.33	7.71-8.55
		30°C	47	8.31	8.15-8.49	7.89-8.72
♂♀	control	28.5°C	35	8.15	7.98-8.32	7.73-8.57
		29.25°C	28	8.41	8.21-8.61	7.92-8.90
		30°C	34	8.86	8.67-9.05	8.38-9.32
	+0.75°C	28.5°C	32	8.45	8.24-8.63	7.96-8.92
		29.25°C	32	8.17	7.90-8.36	7.63-8.73
		30°C	31	8.63	8.43-8.89	8.07-9.20
	+1.5°C	28.5°C	30	8.40	8.20-8.59	7.91-8.87
		29.25°C	29	8.47	8.21-8.67	7.90-9.05
		30°C	36	8.54	8.31-8.73	8.01-9.10
♂♀	control	28.5°C	26	8.55	8.38-8.73	8.12-9.00
		29.25°C	9	8.96	8.67-9.27	8.25-9.72
		30°C	24	8.85	8.65-9.08	8.33-9.39
	+0.75°C	28.5°C	27	8.26	8.07-8.49	7.72-8.75
		29.25°C	9	8.73	8.40-9.12	7.82-9.59
		30°C	28	8.72	8.42-8.93	8.07-9.36
	+1.5°C	28.5°C	32	8.00	7.81-8.21	7.49-8.49
		29.25°C	10	8.92	8.60-9.31	8.04-9.81
		30°C	33	8.58	8.35-8.83	7.95-9.15
♂♀	control	28.5°C	30	7.80	7.60-7.98	7.35-8.27
		29.25°C	22	8.46	8.26-8.69	7.92-9.02
		30°C	25	8.20	7.97-8.41	7.68-8.73
	+0.75°C	28.5°C	27	7.95	7.75-8.19	7.40-8.48
		29.25°C	25	8.03	7.77-8.29	7.40-8.67
		30°C	27	8.29	8.05-8.56	7.66-8.91
	+1.5°C	28.5°C	30	7.75	7.55-7.98	7.22-8.27
		29.25°C	21	7.97	7.73-8.28	7.26-8.63

		30°C	30	8.03	7.75-8.26	7.44-8.67

CI denotes Bayesian credible intervals (analogous to Frequentist confidence intervals). Sex symbols are coloured by the developmental temperature of fathers and mothers (F1 generation) with blue representing present-day control temperature and orange representing +1.5°C.

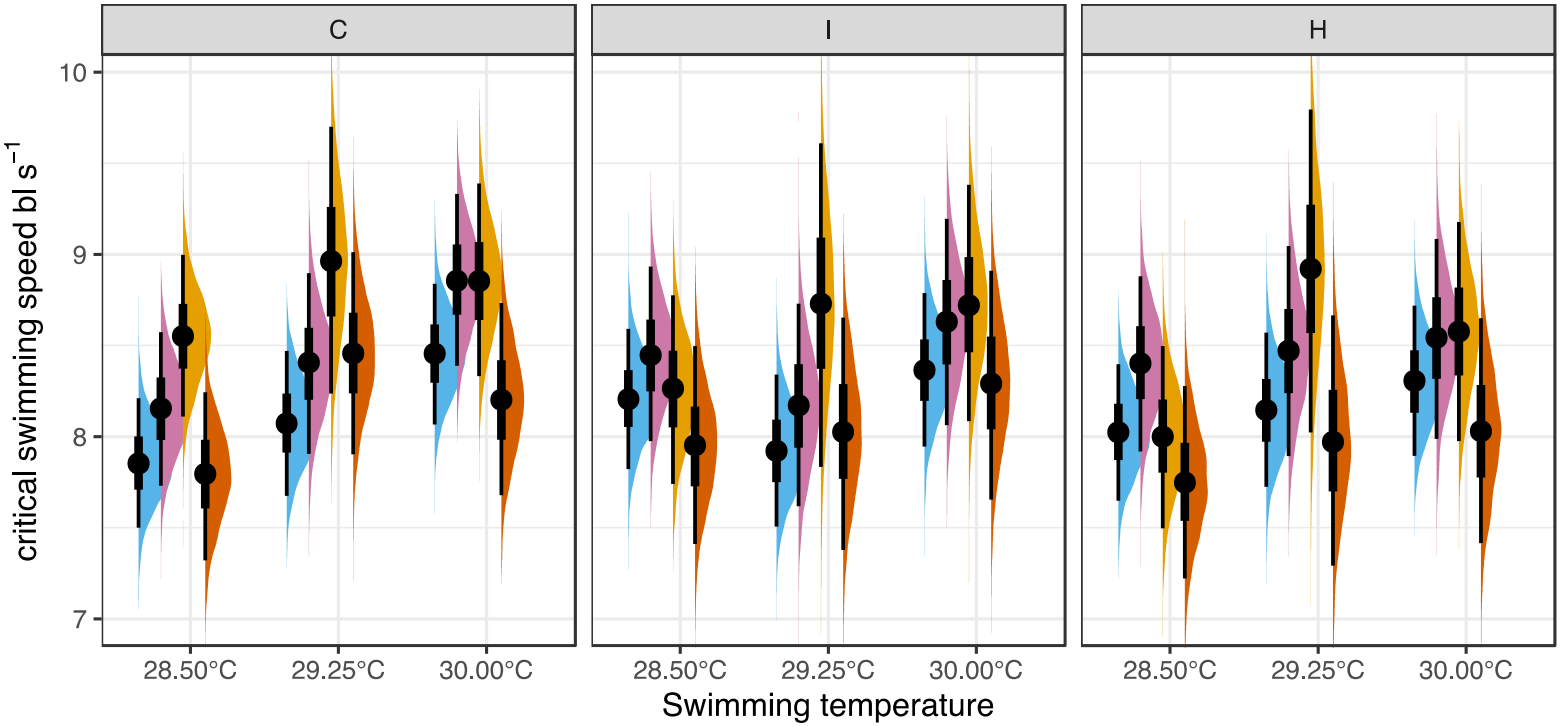


Figure 5.1 Swimming performance. Critical swimming speed in body lengths (bl) s^{-1} of offspring swum at 28.5°C (control), 29.25°C, or 30°C in the four parental and three offspring treatments. The parental treatments from left to right are coloured blue when both parents developed in control (♂♀), pink when only mothers developed in +1.5°C (♂♀), yellow when only fathers developed in +1.5°C (♂♀), or orange when both parents developed in +1.5°C ( ). The offspring treatments are denoted by the banners with C = control, temperature, I = +0.75°C, and H = +1.5°C. Bayesian posterior distributions are shown along with medians (black circles), 50% credible intervals (thick black lines), and 90% credible intervals (thin black lines). Critical swimming speed is presented at the average fish size of 0.41 g cm^{-1}. Note that two thirds fewer fish were swum at 29.25°C (approx. 10 per group), explaining the greater variation.