

Climate change may affect fish through an interaction of parental and juvenile environments

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Abstract Changes to tropical sea surface temperature and plankton communities are expected to occur over the next 100 years due to climate change. There is a limited understanding of how these environmental changes are likely to impact coral reef fishes, especially in terms of population replenishment through the quality of progeny produced. The present study investigated the effect that elevated sea water temperature and changes to food availability may have on the production of offspring by the reef fish *Acanthochromis polyacanthus* (Pomacentridae), as well as the performance of progeny in environments of varying food availability. An orthogonal design of three water temperatures and two food availabilities (high and low ration) was used, with water temperatures being the current-day average for the collection location (28.5 °C), +1.5 °C (30.0 °C) and +3.0 °C (31.5 °C), representing likely temperatures by 2100. Generally, an increase in the water temperature for adults resulted in a reduction in the size, weight and amount of yolk possessed by newly hatched offspring. Offspring whose parents were maintained under elevated temperature (30.0 °C high ration) had lower survival than offspring produced by parents at the current-day temperature (28.5 °C high ration) at 15 days post-hatching, but only when juveniles were reared under

conditions of low food availability. In contrast, by 30 days post-hatching, the growth and condition of these offspring produced by parents held under elevated temperature (30.0 °C high ration) were the best of all treatment groups in all levels of juvenile food availability. This result illustrates the potential for initial parental effects to be modified by compensatory growth early in life (within 1 month) and that parental effects are not necessarily long lasting. These findings suggest that the performance of juvenile reef fish in future ocean conditions may not only depend on initial parental effects, but the interaction between their parentally mediated phenotype and their present food availability.

Keywords Compensatory growth · Coral reef fish · Food availability · Temperature · Parental effects · Survival

Introduction

Substantial changes to tropical oceans are expected to occur within the next century due to climate change. This includes increases in tropical sea surface temperature of up to 3 °C by 2100 (Lough 2007; Munday et al. 2009; Ganachaud et al. 2011) and alterations to ocean currents and surface mixing (Sarmiento et al. 2004; Harley et al. 2006; Rost et al. 2008). Changes to ocean mixing will influence primary productivity leading to flow-on effects to plankton production, which is the major food source for many marine organisms (Hays et al. 2005; Richardson 2008; Rost et al. 2008). In general, the expectation is for less productive tropical oceans due to greater thermal stratification of the water column reducing nutrient enrichment of the surface layers that is important for planktonic productivity (Poloczanska et al. 2007; Brander

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2009). Future changes in food availability will also be superimposed on a resource that is inherently variable on a broad range of spatial and temporal scales. Plankton availability is known to vary temporally at the same location over weeks or months in both quantity and species composition (Rothlisberg and Jackson 1982; McKinnon et al. 2008).

The majority of coral reef organisms, including fishes, are ectotherms. This means their basic metabolic processes are influenced by environmental temperature (Bret 1971; Hazel and Prosser 1974; Houde 1989; Clarke and Johnston 1999). Research on terrestrial ectotherms indicates that tropical species are especially sensitive to increases in environmental temperature because they tend to live close to their thermal optimum and they possess a narrow range of temperatures over which they can perform successfully (Deutsch et al. 2008; Tewksbury et al. 2008; Wright et al. 2009). For aquatic ectotherms, metabolic performance declines as water temperature increases above the thermal optimum. Specifically, the energy required to function at rest (resting metabolic rate) increases, while the ability to perform aerobically decreases (Pörtner and Knust 2007; Pörtner and Farrell 2008; Farrell 2009). These relationships between metabolic attributes and increasing water temperatures have been seen across a range of coral reef fish species (Nilsson et al. 2009, 2010; Gardiner et al. 2010; Johansen and Jones 2011). Since the energy required at rest is increased with warming, it might be expected that organisms will consume more food to compensate (Jobling 1996). However, in food-restricted situations, trade-offs between non-essential activities, such as reproduction and growth, would be expected (Angilletta et al. 2003).

Both temperature and food availability are known to directly affect reproductive attributes in marine fishes. Elevated temperatures can influence the secretion and the action of reproductive hormones (Van Der Kraak and Pankhurst 1997), egg size and number (Brown et al. 2006; Donelson et al. 2010), the frequency of reproduction (Hilder and Pankhurst 2003) and offspring size and quality (Brown et al. 2006; Donelson et al. 2010). Variation in food available to parents can affect the energy available for reproduction, and consequently the number, size, energy content or biochemical composition of the eggs produced (see Green 2008 for review). These variations can have flow-on effects to the size and condition of offspring produced (Kerrigan 1997; McCormick 2003; Gagliano and McCormick 2007; Green 2008) as well as how progeny performs in various environments (Donelson et al. 2009). Studies of the combined effects of temperature and food availability on reproduction and early larval development in tropical marine fish indicate that, in most cases, variation in temperature has a greater effect on the ability to develop and reproduce than variation in food abundance

(Meekan et al. 2003; Donelson et al. 2010). However, when both food availability and thermal environment are unfavourable, the effects to development and reproduction are more pronounced than either single variable in isolation (Donelson et al. 2010).

Differences in offspring characteristics in early ontogeny, whether from parental effects or from previous environments, may be compensated for when their present environment is favourable. For example, compensatory growth is observed in a range of organisms, where smaller individuals can rapidly increase their growth catching up to larger individuals in the cohort (Arendt et al. 2001; Metcalfe and Monaghan 2001; Morgan and Metcalfe 2001; Johnsson and Bohlin 2006; Álvarez and Metcalfe 2007; Gagliano and McCormick 2007). However, this rapid growth can come at a cost to other life-history traits and physical attributes (Arendt et al. 2001; Metcalfe and Monaghan 2001; Morgan and Metcalfe 2001; Álvarez and Metcalfe 2007), potentially leading to poorer survival (Johnsson and Bohlin 2006). Additionally, differences between offspring caused by parental effects may only be important under stressful juvenile environments (Marshall et al. 2006; Donelson et al. 2009). Consequently, predicting the effects that changes in ocean temperature and food supply will have on marine populations is challenging, because it depends both on how the parental environment affects offspring quality and condition, and how these offspring respond to changed environments (Munday et al. 2009). To better understand this problem, we need to investigate how offspring produced by parents maintained under future climate predictions perform when located in different juvenile environments.

In this study, we tested the effects that future predicted ocean temperatures and food availability have on the life-history attributes of offspring produced by pairs of the coral reef fish *Acanthochromis polyacanthus* (Bleeker 1855). We then examined how the offspring performed under different levels of available food. Specifically, we tested the ability of offspring to survive on endogenous reserves, a low, a medium and a high food level, as well as their growth in these environments. By comparing key life-history attributes including growth, condition and survival in different juvenile food levels, the importance of interactions between the parental and juvenile environment in shaping the early life history of reef fish could be established.

Materials and methods

Study species and adult rearing conditions

Forty-two adult pairs of *A. polyacanthus* were collected from the central region of the Great Barrier Reef

(Australia) during the Austral winter and housed in 60-l aquariums at the James Cook University Marine and Aquaculture Research Facility. Breeding pairs were split into three temperature treatments: current-day average temperature (summer mean = 28.5 °C), 30.0 °C (current +1.5 °C) and 31.5 °C (current +3.0 °C). The current-day summer means were calculated from November to February over 14 years of daily water temperature records from the JCU/AIMS weather station. Breeding pairs at each temperature were randomly assigned to two feeding treatments (high or low ration) to produce a fully orthogonal design with 7–8 breeding pairs at each combination of temperature and food ration. The high-food treatments consisted of 0.376 g Aquaculture Nutrition NRD 12/20 pellets (1.0 % body weight) per fish per day, which is approximately the average amount of food consumed by *A. polyacanthus* per day at the collection location (Donelson et al. 2010). The low treatment was half of the high at 0.188 g per fish per day (0.5 % body weight) and represented the minimum amount of food fish were consuming per day (Donelson et al. 2010).

Hatching characteristics

Nesting sites were checked daily for the presence of clutches. On the day of hatching, twenty haphazardly selected juveniles were removed from each clutch for measurement of physical attributes (Table 1). The sampled fish were euthanised with an overdose of clove oil and then preserved in 4 % phosphate-buffered formaldehyde solution. Weight, standard length (SL) and yolk area were measured after 2 days of preservation. SL was estimated by photographing fish under a stereomicroscope and subsequently using image analysis software (Optimus 6.5, Media Cybernetics). The length of each fish and the area of each yolk sac were measured to the nearest 0.01 mm three times, and the average recorded. Fish were then blotted dry and weighed to the nearest mg.

Breeding pairs did not reproduce evenly in all combinations of temperature and food levels, with pairs in both the +1.5 °C and +3.0 °C on low food ration failing to reproduce at all (Donelson et al. 2010). Seven clutches were produced in the 28.5 °C (current day) high-food-

ration treatment, and three clutches in each of the remaining three treatments (28.5 °C low food ration, 30.0 °C (+1.5 °C) high food ration, and 31.5 °C (+3.0 °C) high food ration). In addition, limited numbers of offspring in the 31.5 °C treatment survived through to hatching; thus, post-hatching experiments were unable to be completed in this treatment (Table 1).

Survival on endogenous reserves

Survival on endogenous reserves provides an indication of the quantity and quality of yolk provided by mothers to offspring. To determine whether the length of time offspring can survive on their endogenous resources varied between treatments, a random sample of 20 newly hatched individuals from each clutch was reared without food (Table 1). Juveniles were haphazardly selected from each clutch within 2 h of hatching and transferred to individual 2-l plastic aquariums (260 × 120 × 95 mm) in an environmentally controlled room (as per Donelson et al. 2008). Fish were maintained in the temperature of their parents throughout the experiment. For the current-day treatment, the mean temperature over the experimental period was 28.49 °C (±0.03 SE), and for the +1.5 °C treatment, the mean temperature was 30.11 °C (±0.05 SE). The light regime was kept at the summer average for the parental collection location; 12.75 h light: 12.25 h dark. Each aquarium containing a juvenile was checked daily at approximately 09:00 and 17:00 h to determine whether that individual was still alive.

Juvenile rearing conditions

Sixty juveniles per breeding pair (Table 1) were haphazardly sampled at hatching and transferred into individual 2-l plastic aquariums (160 × 160 × 9 mm) in their corresponding parental temperature and supplied with a constant flow of seawater at temperatures stated above. Twenty of the sixty fish were randomly assigned to each of the three feeding treatments. On the first day of the experiment, all fish were fed *Artemia* nauplii at a concentration of 2 individuals ml⁻¹ (approximately 4,000 individuals per aquaria). Subsequently, they were fed *Artemia* nauplii at a concentration of 2

Table 1 Number of breeding pairs from each parental treatment whose offspring were used in each experiment

	28.5 °C high ration	28.5 °C low ration	30.0 °C high ration	30.0 °C low ration	31.5 °C high ration	31.5 °C low ration
Hatching characteristics	7	3	3	0	3	0
Survival on endogenous reserves	7	3	3	0	0	0
Survival with varying food availability	7	3	3	0	0	0
Growth with varying food availability	7	3	3	0	0	0

individuals ml^{-1} every day (high food treatment), two out of every three days (medium food treatment), or every third day (low food treatment). From day 7 onwards, juveniles were fed *Artemia* at 1 individual ml^{-1} and approximately 2 mg of INVE Aquaculture Nutrition 2/4 NRD pellets at each feed. From day 15 onwards, juveniles were fed approximately 5 mg of INVE Aquaculture Nutrition 2/4 NRD pellets at each feed. Any juveniles that died within the first 24 h after relocation were replaced, as this mortality was attributed to the stress of movement. Subsequently, containers were checked daily at 09:00 h, and deaths within the previous 24-h period were recorded.

Half of the individuals still alive were sampled at day 15 of the experiment (low food $n = 2$ –10, medium food $n = 8$ –10 and high food $n = 7$ –10 per pair), and all the remaining individuals were sampled at day 30 post-hatching (low food $n = 0$ –9, medium food $n = 7$ –10 and high food $n = 6$ –10 per pair). Fish were euthanised and measured on the day of sampling prior to preservation. Fish were photographed under a stereomicroscope using image analysis and SL measured to the nearest 0.01 mm. Fish were then blotted dry with a paper towel and weighed (to nearest mg).

Data analysis

Parental effects on hatching characteristics

To determine whether parental temperature and food level affected offspring characteristics at hatching, a one-factor MANOVA was run on SL, weight, yolk area and Fulton's K condition. In this analysis, parental temperature and food availability were combined as one variable due to the absence of data from the elevated temperatures and low food levels (i.e. only four treatments were compared; 28.5 °C high food ration, 28.5 °C low food ration, 30.0 °C high food ration and 31.5 °C high food ration). Where significant differences were identified, univariate ANOVAs and Fisher's LSD post hoc tests were undertaken. To determine whether parental temperature and food treatment affected survival on endogenous reserves, a multiple-sample survival analysis was used. This analysis is an extension of the Gehan's generalised Wilcoxon test. Where significant differences were found between the survival of juveniles depending on parental treatment, two-sample Cox's F test survival analysis was run on each combination of parental treatments with an adjusted significance level of 0.0167.

Juvenile survival and growth

Separate multiple-sample survival analyses were completed for each juvenile food level. If significant differences were identified between the survival of juveniles

depending on parental treatment, two-sample Gehan's Wilcoxon tests were run with adjusted significance levels of 0.0167. To investigate whether parental treatment and juvenile food level affected growth of juveniles, a factorial MANOVA was undertaken on SL, weight and Fulton's K condition separately at 15 and 30 days post-hatching. At 15 days post-hatching, SL and weight were log-transformed to meet the assumption of homogeneous variances. ANOVAs and Fisher's LSD post hoc tests were used to explore the nature of significant MANOVAs. All statistical analyses were completed using Statistica 9.0.

Results

Hatching characteristics

The physical characteristics of individuals at hatching depended on their parents' temperature and food treatment (Fig. 1; MANOVA: $F_{12,828} = 15.7$, $p < 0.001$; univariate: SL— $F_{3,277} = 25.11$, $p < 0.001$, weight— $F_{3,277} = 18.68$, $p < 0.001$, yolk area— $F_{3,277} = 22.78$, $p < 0.001$, condition— $F_{3,277} = 22.78$, $p < 0.001$). Both SL and weight declined with increasing parental temperature (Fig. 1a, b; $p < 0.004$), while offspring from parents in the 28.5 °C low-food-ration treatment were longer than offspring from parents in any of the high-food-ration treatments ($p < 0.001$). Yolk area was smallest in offspring from parents in the 30.0 °C high-food-ration treatment (Fig. 1c; $p < 0.001$), but still significantly less in offspring from parents in the 31.5 °C high-ration and 28.5 °C low-ration treatments compared to the 28.5 °C high-food-ration treatment ($p < 0.03$). Contrastingly, the condition of offspring from parents in the three high-food-ration treatments was similar ($p > 0.05$) and only significantly reduced in the 28.5 °C low-food-ration treatment (Fig. 1d; $p < 0.002$).

Survival on endogenous reserves

The combination of parental temperature and food level significantly influenced the rate of offspring mortality on endogenous reserves (Fig. 2; $\chi^2 = 84.73$, $df = 2$, $p < 0.001$). Offspring produced by parents on the high food ration in 28.5 °C survived up to 4 days longer (up to 13 days post-hatching) than offspring from parents in the 28.5 °C low-food-ration treatment (Cox's F test: $F_{278,120} = 3.806$, $p < 0.001$) and from parents in the 30.0 °C high-food-ration treatment (Cox's F test: $F_{278,120} = 2.790$, $p < 0.001$). Offspring from parents in the 30.0 °C high-food-ration and the 28.5 °C low-food-ration treatments survived a maximum of 10 days post-hatching and were not significantly different (Cox's F test: $F_{120,120} = 1.457$, $p > 0.0167$).

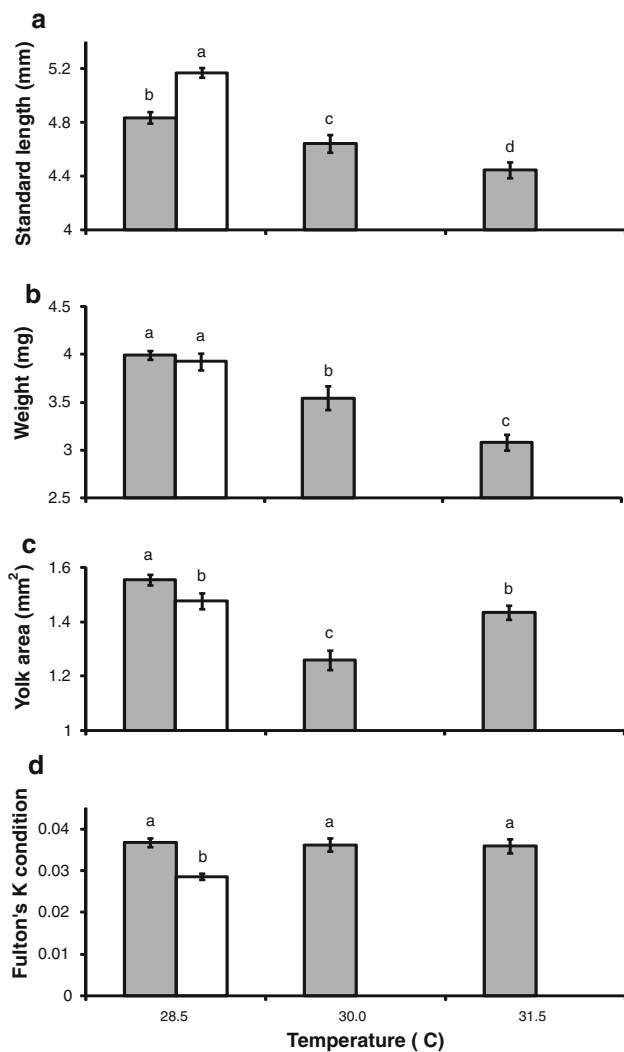


Fig. 1 Mean standard length (a), weight (b), yolk area (c) and (d) Fulton's K condition index (\pm SE) of newly hatched *A. polyacanthus* that resulted from breeding pairs kept under a combination of three water temperatures and two food ration levels. Shaded bars high food ration levels; white bars low food ration levels. Letters over bars represent the groupings from Fisher's LSD post hoc tests ($p < 0.05$)

Juvenile survival under different food availability

Greater than 85 % survival occurred in the high and medium ration juvenile food treatments regardless of parental treatment over the first 15 days post-hatching (Fig. 3a, b). In contrast, up to 70 % mortality occurred in the low ration juvenile food treatment (Fig. 3c). Furthermore, in the low ration juvenile food treatment, differences in offspring survival depended on parental treatment ($\chi^2 = 7.93$, $df = 2$, $p = 0.019$). Offspring from parents in the 28.5 °C high-food-ration treatment had on average 69 % survivorship at day 15 and survived significantly better than offspring from 28.5 °C low-food-ration parents

($z = 3.839$, $n = 200$, $p < 0.001$) and from 30.0 °C high-food-ration parents at ($z = 5.218$, $n = 200$, $p < 0.001$). However, no differences were seen between the survival of offspring from 28.5 °C low-food-ration parents (mean, 42 % on day 15) and 30.0 °C high-food-ration parents (mean, 32 % on day 15; $z = 1.717$, $n = 120$, $p = 0.086$). In the medium ration juvenile food treatment, no differences were seen in survival among parental treatments ($\chi^2 = 0.790$, $df = 2$, $p = 0.674$). In contrast, in the high ration juvenile food treatment, offspring from parents in the 28.5 °C low-food-ration treatment had significantly greater mortality levels than offspring from parents in the 30.0 °C high-food-ration treatment (full model: $\chi^2 = 7.93$, $df = 2$, $p = 0.019$; 30.0 °C high: $z = 2.451$, $n = 120$, $p = 0.014$).

Growth in various food quality environments

Juvenile growth and condition were strongly affected by the food level available at both 15 days (Table 2; MANOVA: $F_{6,584} = 51.0$, $p < 0.001$; univariate: SL— $F_{2,301} = 236.0$, $p < 0.001$; Weight— $F_{2,231} = 276.6$, $p < 0.001$; Fulton's K condition— $F_{2,301} = 21.17$, $p < 0.001$) and 30 days post-hatching (Table 3; MANOVA: $F_{6,444} = 44.64$, $p < 0.001$; univariate: SL— $F_{2,231} = 135.15$, $p < 0.001$; Weight— $F_{2,231} = 143.70$, $p < 0.001$; Fulton's K condition— $F_{2,231} = 5.65$, $p = 0.004$). The importance of the parental environment (combined temperature and food level) differed depending on the attribute measured and the time post-hatching. At 15 days, parental environment did not significantly influence SL ($F_{2,301} = 2.30$, $p = 0.101$), but did affect weight ($F_{2,301} = 3.89$, $p = 0.022$) and interacted with juvenile food level to affect condition ($F_{2,301} = 3.98$, $p = 0.004$; Table 2). Specifically, the weight of fish from 28.5 °C low-food-ration parents was less than both other parental treatments ($p < 0.007$). Body condition did not differ between any parental treatment in the low juvenile food ration treatment, but in the medium juvenile food ration treatment, offspring from 28.5 °C high-food-ration parents performed significantly better ($p < 0.03$), and in high juvenile food ration treatment, offspring from 28.5 °C low-food-ration parents were in significantly worse condition ($p < 0.001$). At 30 days post-hatching, the parental treatment significantly affected SL ($F_{2,231} = 4.11$, $p = 0.018$), weight ($F_{2,231} = 3.31$, $p = 0.038$) and body condition (Table 3; $F_{2,231} = 6.23$, $p = 0.002$). However, offspring from various parental treatments performed differently depending on the attribute measured. Offspring produced by 28.5 °C high-food-ration parents were in the poorest condition at 30 days ($p < 0.009$), while offspring from 28.5 °C low-food-ration parents were significantly shorter ($p < 0.016$) and offspring from 30.0 °C high-food-ration parents were significantly heavier than both other groups ($p = 0.004$).

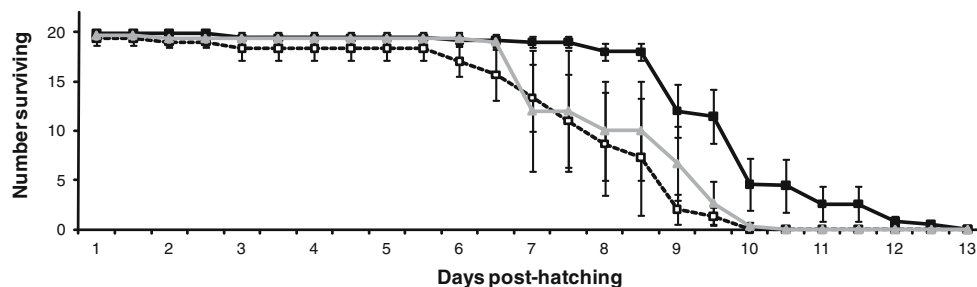


Fig. 2 Mean survival (\pm SE) of juvenile *A. polyacanthus* on endogenous reserves in relation to parental maintenance temperature and food ration level. *Black squares*, parents kept under 28 °C and high

food ration; *open squares*, parents under 28 °C and low food ration; *grey triangles*, parents under 30 °C and high food ration

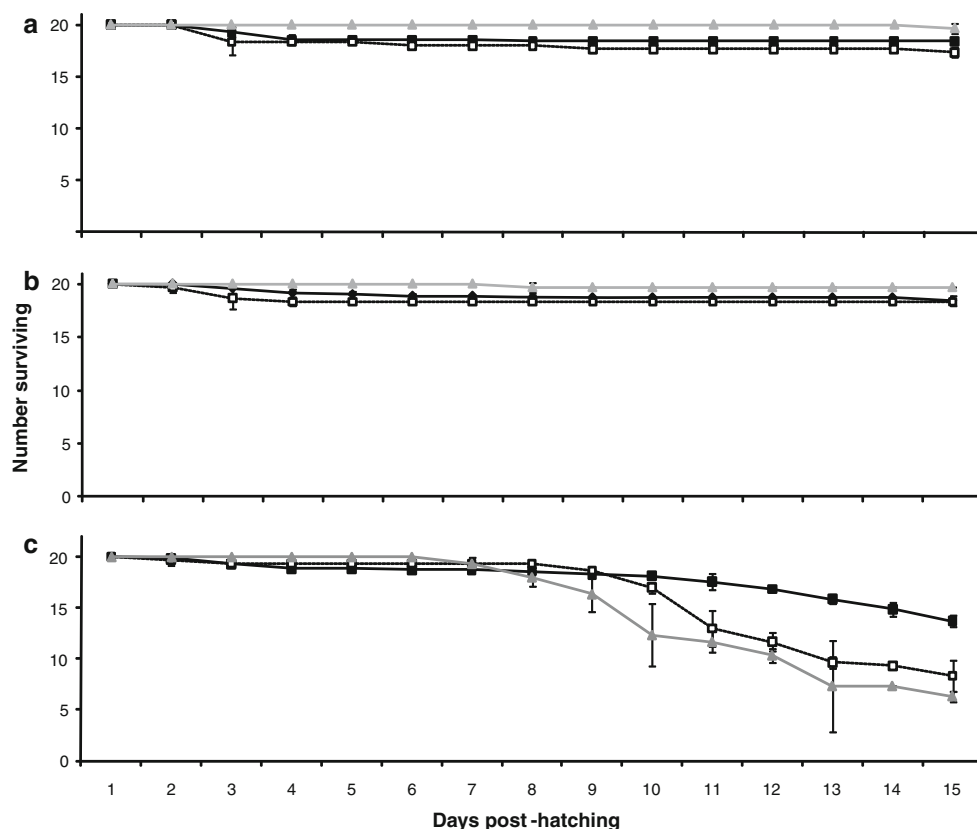


Fig. 3 Mean survival (\pm SE) of juvenile *A. polyacanthus* reared under three conditions: **a** Juvenile high food ration, **b** juvenile medium food ration and **c** juvenile low-food-ration environments. Survival is plotted in relation to parental maintenance temperature

and food ration level. *Black squares*, parents kept under 28 °C and high food ration; *open squares*, parents under 28 °C and low food ration; *grey triangles*, parents under 30 °C and high food ration

Discussion

Evidence of parental effects on offspring characteristics at hatching was found when parents were maintained in future predicted temperature and food conditions. As the temperature experienced by parents increased, the size of offspring became smaller and yolk reserves declined. The performance of these juveniles reared with differing access to food depended on their parental treatment; however, performance was not always consistent with offspring

characteristics at hatching. Offspring from parents kept under 30.0 °C, and high-food-ration conditions were smaller at hatching, but by 30 days post-hatching were generally longer, heavier and in better condition. In contrast, offspring from 28.5 °C low-food-ration parents were largest at hatching, but smallest by 30 days. When poor juvenile food levels were present, the survival of offspring from 30.0 °C high-food-ration parents and from 28.5 °C low-food-ration parents was significantly worse than that of offspring from 28.5 °C high-food-ration parents. This

Table 2 Effect of parental treatment (breeding temperature and food ration) and juvenile food ration on standard length, weight and Fulton's K condition at 15 days post-hatching *A. polyacanthus*

	Parental treatment		
	28.5 °C high ration	28.5 °C low ration	30.0 °C high ration
Juvenile high ration	SL = 8.48 ± 0.08	SL = 8.42 ± 0.12	SL = 8.44 ± 0.14
	Weight = 18.62 ± 0.49	Weight = 16.67 ± 0.68	Weight = 17.90 ± 0.82
	Condition = 0.030 ± 0.0005	Condition = 0.027 ± 0.0005	Condition = 0.029 ± 0.0006
Juvenile medium ration	SL = 7.53 ± 0.05	SL = 7.48 ± 0.09	SL = 7.47 ± 0.12
	Weight = 12.61 ± 0.33	Weight = 11.56 ± 0.49	Weight = 11.50 ± 0.59
	Condition = 0.029 ± 0.0004	Condition = 0.027 ± 0.0006	Condition = 0.027 ± 0.0006
Juvenile low ration	SL = 6.27 ± 0.06	SL = 5.94 ± 0.15	SL = 6.37 ± 0.17
	Weight = 5.91 ± 0.22	Weight = 5.42 ± 0.56	Weight = 6.86 ± 0.70
	Condition = 0.024 ± 0.0005	Condition = 0.025 ± 0.0012	Condition = 0.026 ± 0.0014

Values are mean ± SE

Table 3 Effect of parental treatment (breeding temperature and food ration) and juvenile food ration on standard length, weight and Fulton's K condition at 30 days post-hatching *A. polyacanthus*

	Parental treatment		
	28.5 °C high ration	28.5 °C low ration	30.0 °C high ration
Juvenile high ration	SL = 12.67 ± 0.20	SL = 12.16 ± 0.21	SL = 12.84 ± 0.32
	Weight = 61.17 ± 2.71	Weight = 57.21 ± 3.19	Weight = 68.17 ± 5.14
	Condition = 0.030 ± 0.0004	Condition = 0.028 ± 0.0005	Condition = 0.031 ± 0.0007
Juvenile medium ration	SL = 11.26 ± 0.16	SL = 10.60 ± 0.19	SL = 11.01 ± 0.26
	Weight = 41.68 ± 1.78	Weight = 36.46 ± 1.85	Weight = 44.8 ± 3.14
	Condition = 0.029 ± 0.0003	Condition = 0.030 ± 0.0006	Condition = 0.033 ± 0.0006
Juvenile low ration	SL = 8.24 ± 0.33	SL = 7.66 ± 0.30	SL = 8.33 ± 0.38
	Weight = 15.45 ± 2.22	Weight = 12.75 ± 1.97	Weight = 16.9 ± 2.64
	Condition = 0.027 ± 0.001	Condition = 0.027 ± 0.0022	Condition = 0.028 ± 0.0014

Values are mean ± SE

suggests that progeny performance in future ocean conditions will not only depend on their environment, but the interaction between their parentally mediated phenotype and their present environment.

For coral reef fish, the first few weeks of life are known to be critical for success and small differences in body size and growth rate may substantially influence survival (Sale and Ferrell 1988; Almany and Webster 2006). In our experiments, parents maintained in future predicted temperatures produced smaller and lighter offspring with less yolk provisioning. Mortality is size selective in juvenile reef fish, and consequently, offspring produced by parents in future warmer oceans may suffer greater mortality than current-day individuals if it takes longer for mortality size thresholds to be reached (Bergenius et al. 2002; Holmes and McCormick 2009). Body condition has also been identified as a potential determinant of survival during the early life of reef fish (Hoey and McCormick 2004; Holmes and McCormick 2009), and the condition of offspring from

all high-ration parents was similar regardless of increasing temperature. Thus, the early juvenile survival in future populations will depend on the nature of selectivity agents and what offspring traits are most influential; traits that are important in future may not be the same as current day.

Generally, elevations in parental environmental temperature had a greater effect on the attributes of offspring at hatching than in parental food levels. Specifically, an increase of only 1.5 °C caused a greater reduction in offspring size and yolk reserves than half the food provisioning to parents. It may also indicate that temperature directly affects reproductive pathways that influence gamete quality (final oocyte maturation and vitellogen production; Pankhurst et al. 1996; King et al. 2007) and consequently offspring attributes. There is substantial support for elevations in temperature negatively affecting reproductive pathways and production of gametes of marine fishes (Manning and Kime 1985; Pankhurst and Thomas 1998; Van der Kraak and Pankhurst 1997; Hilder and

Pankhurst 2003; Pankhurst and Porter 2003), and this occurred in breeding adults utilised in the present study (Donelson et al. 2010).

The importance of parental effects on offspring survival differed depending on the food available to juveniles. Juvenile survival depended on parental treatment when there was a low-level or no food provided (survival on endogenous reserves) in the juvenile environment. In these poor environments, offspring from 28.5 °C high-food-ration parents survived significantly better than offspring from parents that experienced an increase of +1.5 °C or a reduction in food availability. Offspring from parents maintained under 28.5 °C low food ration or 30.0 °C high food ration survived similarly in these poor juvenile conditions, suggesting that a 1.5 °C increase or half the food available to parents may produce comparable offspring survival in future. In contrast, in moderate and high juvenile food levels, the trend of better survival by offspring of 28.5 °C high-food-ration parents was lost, supporting the hypothesis that parental effects play an important role when offspring are in food-limited or competitive environments (Marshall et al. 2006; Donelson et al. 2009). However, a large amount of research shows that parental effects are more influential at the beginning of life and over weeks to months the current environment of offspring becomes more influential (Donelson et al. 2009; van der Sman et al. 2009). Interestingly, offspring from the two parental treatments (28.5 °C low food ration and 30.0 °C high food ration) that survived similarly in poor juvenile food levels (low or no food) exhibited significantly different survival rates under high juvenile food availability, with fish produced by 30.0 °C parents surviving significantly better than fish produced by 28.5 °C parents. This suggests that the way parental effects affect progeny survival can depend on juvenile food availability.

It is well established that the amount of food available to a juvenile will substantially influence their growth and condition (Jones 1986; Forrester 1990; Booth and Alquezar 2002). Our data fitted the expected trends with juveniles being longer, heavier and in better body condition with increasing food availability. However, offspring performance within these food availabilities depended on their parent's temperature and feeding history. At 15 days post-hatching with low food availability, juveniles from all parental treatments grew similarly, whereas at moderate and high food levels, larval growth was affected by parental treatment. This observation is in contrast to previous findings that beneficial parental effects are only important in poor quality environments (Donelson et al. 2009). However, our ability to detect differences between parental groups in the low food juvenile environment may have been limited by high juvenile mortality.

By 30 days post-hatching offspring from 30.0 °C parents were generally performing the best for all physical attributes measured. Initially, at hatching, these offspring were shorter and lighter than offspring produced by either 28.5 °C parental group. This indicates that while fish started out with potential physical limitations, they were able to compensate for differences across all juvenile food environments (Arendt et al. 2001; Morgan and Metcalfe 2001; Johnsson and Bohlin 2006; Álvarez and Metcalfe 2007; Gagliano and McCormick 2007). Even when food availability was low and mortality was significantly greater for offspring from 30.0 °C high-food-ration parents, individuals that persisted from this treatment were in better condition compared to juveniles from the 28.5 °C high- and low-food-ration treatments. In contrast, offspring produced by 28.5 °C low-food-ration parents were the longest at hatching, but by 30 days, were significantly shorter than the two other parental treatments. These findings suggest that initial measures of size and condition may be good indicators of growth and survival when fish first arrive on the reef (Hoey and McCormick 2004; Holmes and McCormick 2009), but other phenotypic parental contributions not captured by size and condition estimates may subsequently determine performance (e.g. yolk quality or hormones). Additionally, a portion of the difference in growth and condition observed between 28.5 and 30.0 °C treatments may be directly due to the temperature differences of the juvenile environment, since offspring were carried through on their parent's temperature. Small increases in temperature are known to enhance growth and development rate (Rombough 1997; Meekan and Fortier 1996; Bergenius et al. 2002; Wilson and Meekan 2002; Sponaugle et al. 2006). However, for this to be the only cause of differences between offspring from 28.5 and 30.0 °C high-food-ration parents, juveniles reared at 30.0 °C would have been expected to be unable to maintain a high rate of growth and condition under low-food-ration conditions in the juvenile environment.

This study highlights the potential impacts that elevated sea temperature and reductions in food availability to adults will have on their progeny. Some of these parental effects on progeny will determine juvenile survival in times of low food availability. The study illustrates that observed differences in hatching characteristics caused by moderate ocean warming (+1.5 °C and no reduction in food) are able to be compensated for over relatively short time frames (15–30 days). To determine the long-term effects of differences in hatching characteristics and compensatory growth, longer running grow-out experiments are required. While the model species used in the present study possesses an atypical early life history, our results are likely to be general across a range of species since parental effects and the environment during early life can significantly

influence the success of juveniles (Meekan et al. 2003; Hoey and McCormick 2004; Green 2008). The potential for long-term thermal acclimation has not been tested in this study, and the importance of parental effects to offspring may be altered when fish live their whole life under future climate conditions.

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References

- Almany GR, Webster MS (2006) The predation gauntlet: early post-settlement mortality in reef fishes. *Coral Reefs* 25:19–22
- Álvarez D, Metcalfe NB (2007) The tradeoff between catch-up growth and escape speed: variation between habitats in the cost of compensation. *Oikos* 116(1144):1151
- Angilletta MJ Jr, Wilson RS, Navas CA, James RS (2003) Tradeoffs and the evolution of thermal reaction norms. *Trends Ecol Evol* 18:234–240
- Arendt J, Wilson DS, Stark E (2001) Scale strength as a cost of rapid growth in sunfish. *Oikos* 93:95–100
- Bergenius MAJ, Meekan MG, Robertson R, McCormick MI (2002) Larval growth predicts recruitment success of a coral reef fish. *Oecologia* 131:521–525
- Booth D, Alquezar R (2002) Food supplementation increases larval growth, condition and survival of *Acanthochromis polyacanthus*. *J Fish Biol* 60:1126–1133
- Brander K (2009) Impacts of climate change on fisheries. Impacts of climate change on fisheries. *J Mar Syst* 79:389–402
- Bret JR (1971) Energetic responses of salmon to temperature. A study in some thermal relations in the physiological and freshwater ecology of stockeye salmon (*Oncorhynchus nerka*). *Am Zool* 11:99–113
- Brown NP, Shields RJ, Bromage NR (2006) The influence of water temperature on spawning patterns and egg quality in the Atlantic halibut (*Hippoglossus hippoglossus* L.). *Aquaculture* 261:993–1002
- Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *J Anim Ecol* 68:893–905
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci USA* 105:6668–6672
- Donelson JM, McCormick MI, Munday PL (2008) Parental condition affects early life-history of a coral reef fish. *J Exp Mar Biol Ecol* 360:109–116
- Donelson JM, Munday PL, McCormick MI (2009) Parental effects on offspring life histories: when are they important? *Biol Lett* 5:262–265
- Donelson JM, Munday PL, McCormick MI, Pankhurst NW, Pankhurst PM (2010) Effects of elevated water temperature and food availability on the reproductive performance of a coral reef fish. *Mar Ecol Prog Ser* 401:233–245
- Farrell AP (2009) Environment, antecedents and climate change: lessons from the study of temperature physiology and river migration of salmonids. *J Exp Biol* 212:3771–3780
- Forrester GE (1990) Factors influencing the juvenile demography of a coral reef fish. *Ecology* 71:1666–1681
- Gagliano M, McCormick MI (2007) Maternal condition influences phenotypic selection on offspring. *J Anim Ecol* 76:174–182
- Ganachaud AS, Gupta AS, Orr JC, Wijffles SE, Ridgway KR, Hemer MA, Maes C, Steinberg CR, Tribollet AD, Qiu B, Kruger JC (2011) Observed and expected changes to the tropical Pacific Ocean. In: Bell JD, Johnson JE, Hobday AJ (eds) Vulnerability of Tropical Pacific fisheries and aquaculture to climate change. Secretariat of the Pacific Community, Noumea, pp 101–187
- Gardiner NM, Munday PL, Nilsson GE (2010) Counter-gradient variation in respiratory performance of coral reef fishes at elevated temperatures. *PLoS ONE* 5:1–13
- Green BS (2008) Maternal effects in fish populations. *Adv Mar Biol* 54:1–105
- Harley CDG, Randall Hughes A, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, Rodriguez LF, Tomanek L, Williams SL (2006) The impacts of climate change in coastal marine systems. *Ecol Lett* 9:228–241
- Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. *Trends Ecol Evol* 20:337–344
- Hazel JR, Prosser CL (1974) Molecular mechanism of temperature compensation in poikilotherms. *Physiol Rev* 54:620–677
- Hilder ML, Pankhurst NW (2003) Evidence that temperature change cues reproductive development in the spiny damselfish, *Acanthochromis polyacanthus*. *Environ Biol Fish* 66:187–196
- Hoey AS, McCormick MI (2004) Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. *Oecologia* 139:23–29
- Holmes TH, McCormick MI (2009) Influence of prey body characteristics and performance on predator selection. *Oecologia* 159:401–413
- Houde ED (1989) Comparative growth, mortality and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fish Bull* 87:471–495
- Jobling M (1996) Temperature and growth: modulation of growth rate via temperature change. In: Wood CM, McDonald DG (eds) Global warming: implications for freshwater and marine fish. Cambridge University Press, Cambridge, pp 225–253
- Johansen JL, Jones GP (2011) Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. *Global Change Biol* 17:2971–2979
- Johnsson JI, Bohlin T (2006) The cost of catching up: increased winter mortality following structural growth compensation in the wild. *Proc R Soc Lond B Biol Sci* 273:1281–1286
- Jones GP (1986) Food availability affects growth in a coral reef fish. *Oecologia* 70:136–139
- Kerrigan BA (1997) Variability in larval development of the tropical reef fish *Pomacentrus amboinensis* (Pomacentridae): the parental legacy. *Mar Biol* 127:395–402
- King HR, Pankhurst NW, Watts M (2007) Reproductive sensitivity to elevated water temperatures in female Atlantic salmon is heightened at certain stages of vitellogenesis. *J Fish Biol* 70:90–205
- Lough J (2007) Climate and climate change on the Great Barrier Reef. In: Johnson JE, Marshall PA (eds) Climate change and the Great Barrier Reef: a vulnerability assessment. Great Barrier Reef Marine Park Authority, Townsville, pp 15–50
- Manning NJ, Kime DE (1985) The effect of temperature on testicular steroid production in the rainbow trout, *Salmo gairdneri*, in vivo and in vitro. *Gen Comp Endocrinol* 57:377–382
- Marshall DJ, Cook CN, Emler RB (2006) Offspring size effects mediate competitive interactions in a colonial marine invertebrate. *Ecology* 87:214–225
- McCormick MI (2003) Consumption of coral propagules after mass spawning enhances larval quality of damselfish through maternal effects. *Oecologia* 136:37–45

- McKinnon AD, Duggan S, Carleton JH, Böttger-Schnack R (2008) Summer planktonic copepod communities of Australia's North West Cape (Indian Ocean) during the 1997–99 El Niño/La Niña. *J Plankton Res* 30(839):855
- Meekan MG, Fortier L (1996) Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. *Mar Ecol Prog Ser* 137:25–37
- Meekan MG, Carleton JH, McKinnin KF, Furnas M (2003) What determines the growth of tropical reef fish larvae in the plankton: food or temperature? *Mar Ecol Prog Ser* 256:193–204
- Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? *Trend Ecol Evol* 16:254–260
- Morgan IJ, Metcalfe NB (2001) Deferred costs of compensatory growth after autumnal food shortage in juvenile salmon. *Proc R Soc Lond B Biol Sci* 268:295–301
- Munday PL, Leis JM, Lough JM, Paris CB, Kingsford MJ, Berumen ML, Lambrechts J (2009) Climate change and coral reef connectivity. *Coral Reefs* 28:379–395
- Nilsson GE, Crawley N, Lunde IG, Munday PI (2009) Elevated temperature reduces the respiratory scope of coral reef fishes. *Global Change Biol* 15:1405–1412
- Nilsson GE, Östlund-Nilsson S, Munday PL (2010) Effects of elevated temperature on coral reef fishes: loss of hypoxia tolerance and inability to acclimate. *Comp Biochem Physiol Part A* 156:389–393
- Pankhurst NW, Porter MJR (2003) Cold and dark warm and light: variations on the theme of environmental control of reproduction. *Fish Physiol Biochem* 28:385–389
- Pankhurst NW, Thomas PM (1998) Maintenance at elevated temperature delays the steroidogenic and ovulatory responsiveness of rainbow trout *Oncorhynchus mykiss* to luteinizing hormone releasing hormone analogue. *Aquaculture* 166:163–177
- Pankhurst NW, Purser GJ, Van Der Kraak G, Thomas PM, Forteach GNR (1996) Effect of holding temperature on ovulation, egg fertility, plasma levels or reproductive hormones and in vitro ovarian steroidogenesis in the rainbow trout *Oncorhynchus mykiss*. *Aquaculture* 146:277–290
- Poloczanska ES, Babcock RC, Butler A, Hobday A, Hoegh-Guldberg O, Kunz TJ, Matear R, Milton DA, Okey TA, Richardson AJ (2007) Climate change and Australian marine life. *Oceanogr Mar Biol Annu Rev* 45:407–478
- Pörtner HO, Farrell AP (2008) Physiology and climate change. *Science* 322:690–692
- Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315:95–97
- Richardson AJ (2008) In hot water: zooplankton and climate change. *ICES J Mar Sci* 65:279–295
- Rombough PJ (1997) The effects of temperature on embryonic and larval development. In: Wood CM, McDonald DG (eds) *Global warming: implications for freshwater and marine fish*. Cambridge University Press, Cambridge, pp 177–223
- Rost B, Zondervan I, Wolf-Gladrow D (2008) Sensitivity of phytoplankton to future changes in ocean carbonate chemistry: current knowledge, contradictions and research directions. *Mar Ecol Prog Ser* 373:227–237
- Rothlisberg PC, Jackson CJ (1982) Temporal and spatial variation of plankton abundance in the Gulf of Carpentaria, Australia 1975–1977. *J Plankton Res* 4:19–40
- Sale PF, Ferrell DJ (1988) Early survivorship of juvenile coral-reef fishes. *Coral Reefs* 7:117–124
- Sarmiento JL, Slater R, Barber R, Bopp L, Doney SC, Hirst AC, Kleypas J, Matear R, Mikolajewicz U, Monfray P, Soldatov V, Spall SA, Stouffer R (2004) Response of ocean ecosystems to climate warming. *Global Biochem Cycles* 18:1–19
- Sponaugle S, Grorud-Colvert K, Pinkard D (2006) Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida Keys. *Mar Ecol Prog Ser* 308:1–15
- Tewksbury JJ, Huey RB, Deutsch CA (2008) Putting heat on tropical animals. *Science* 320:1296–1297
- Van Der Kraak G, Pankhurst NW (1997) Temperature effects on the reproductive performance of fish. In: Wood CM, McDonald DG (eds) *Global warming: implications for freshwater and marine fish*. Cambridge University Press, Cambridge, pp 159–176
- van der Sman J, Phillips NE, Pfister CA (2009) Relative effects of maternal and juvenile food availability for a marine snail. *Ecology* 90:3119–3125
- Wilson DT, Meekan MG (2002) Growth-related advantages for survival to the point of replenishment in the coral reef fish *Stegastes partitus* (Pomacentridae). *Mar Ecol Prog Ser* 231:247–260
- Wright SJ, Muller-Landau HC, Schipper J (2009) The future of tropical species on warmer planet. *Conserv Biol* 23:1418–1426