Temperature-dependent differences in male and female life history responses to a period of food limitation during development

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Abstract

With climate change, animals face both rising temperatures and more variable food availability. Many species have evolved an adaptative response to historic variation in food availability: they grow faster after a period of diet restriction (“compensatory growth”). However, higher temperatures may reduce the capacity for compensatory growth in ectotherms because individuals require more resources to support their increased metabolism. We experimentally tested how higher temperature affects compensatory growth by raising guppies (*Poecilia reticulata*) at a high or control temperature, and on a normal or temporarily restricted diet during early development. At the control temperature guppies on the restricted diet grew faster once their diet returned to normal. Both sexes showed compensatory growth. At the high temperature, both sexes also increased their growth rates after dietary restriction ended, but the life history outcomes differed. Males at the high temperature matured earlier and were smaller than males reared at the control temperature. In contrast, females at the high temperature matured later and were bigger than females at the control temperature. Our study highlights that rising temperatures could reduce the ability of fish to compensate for periods of low food availability, and that males and females can have different responses to the same environmental stressors.

Introduction

Early environmental conditions play an important role in shaping animal development (1,2). During development animals need to balance food acquisition between allocation to body maintenance and growth (3). However, natural variation in prey availability, population density and predation risk can all affect the ability of animals to acquire food during early development (4–6). Reduced food intake can lower the allocation of resources towards growth resulting in smaller adults that tend to have a higher rate of mortality and lower reproductive success (7,8). To minimise the impact of reduced food intake during development, many species have evolved an adaptive physiological response whereby they grow faster after a period of low food acquisition (so-called ‘compensatory growth’).

Compensatory growth occurs in many taxa that have a wide range of life-history strategies (9). Compensatory growth can be achieved through an increased feeding rate or physiological changes that improve the efficiency of food conversion (10). By accelerating growth after a period of diet restriction, individuals can reach a similar size to age-matched conspecifics that have not experienced a restricted diet (i.e. full compensatory growth). Full compensatory growth is particularly beneficial when time constraints (e.g., growth ceases at maturity) or intense sexual competition favour larger size at maturation (9,11,12). However, compensatory growth can have costs for some components of fitness. For instance, faster growth can impose short-term ecological and physiological costs (e.g., greater exposure to predators and more oxidative damage during development (13–15), as well as long-term ‘hidden’ costs, such as reduced adult mobility, cognition, reproduction and lifespan

(1,11,14,16,17). Compensatory growth has been well documented (9,10), but it remains unclear how it is affected by environmental factors that influence bioenergetic trade-offs, most notably temperature (1).

Temperature is a key factor affecting developmental growth in ectotherms (18). Higher temperatures generally increase metabolic rates, which tends to accelerate development (19,20). Ectotherms developing at warmer temperatures usually mature faster and tend to be smaller (20–22) (the ‘temperature-size rule’ (23)). In addition, higher temperatures can increase the costs of somatic maintenance due to faster accumulation of oxidative damage (24). Consequently, organisms that experience both high temperatures and limited access to food during development likely face an increased challenge to allocate resources to allow for compensatory growth while still ensuring effective somatic maintenance (1). High temperatures are therefore expected to exacerbate the costs of compensatory growth (25–27).

Growth patterns have been extensively studied in aquatic organisms, including fish, because of the economic implications (28–30). Several studies show that fish exhibit full or partial compensatory growth after a period of diet restriction (reviewed in 30). Partial compensatory growth refers to cases where there is faster growth after dietary restriction ends, but animals mature at a smaller size than those on an unrestricted diet. To date, only a few studies have investigated how higher temperatures affect compensatory growth. These studies have mostly focused on temperate species (31–36), which makes their relevance to tropical species uncertain.

Tropical fish live at temperatures near their upper thermal limit and are expected to be more sensitive to increased temperatures than temperate species that usually have a wider thermal tolerance range (37,38). Guppies (*Poecilia reticulata*; Family: Poecilidae) are a tropical fish species that have become a model system for studies in ecology and evolution (39). In guppies, low food availability during development can have long-term effects on somatic and reproductive traits (40–43). Guppies also show compensatory growth after diet restriction during early development, leading to a later decline in fecundity (44). Guppies are therefore an ideal species to test if higher than normal temperatures lower the ability of tropical fish to exhibit compensatory growth after a poor start in life.

Here we test if a higher temperature affects the response to diet restriction by guppies (*P. reticulata*). In a 2x2 experiment we reared fish to maturation at either 26° or 30°C (air temperature; for water see *Methods*) and we manipulated juvenile food availability (control or restricted diet for two weeks). We measured initial and overall juvenile growth, time to maturation and size at maturation. We discriminate between initial growth shortly after a period of food restricted ends, and longer-term growth to maturity. Faster initial growth is used to determine whether compensatory growth occurred. Based on studies of other poecilids (44–48), we predicted that:

(1) At the control temperature (26°C), fish will show compensatory growth after two weeks of diet restriction. At the high temperature (30°C), however, fish will not show compensatory growth after two weeks of diet restriction.
(2) For fish on the control diet, those at the higher temperature will mature earlier and will be smaller than those at the control temperature.
(3) For fish on the restricted diet for two weeks, those at the higher temperatures will mature later but will be smaller than fish on the restricted diet at the control temperature because increased metabolic costs at a higher temperature reduce the energy/resources available for growth.
(4) The size difference at maturity between fish on the control and restricted diet will be greater at the higher temperature than at the control temperature.

Methods

Origin and maintenance of fish

Guppy stocks are from two independent collections from an invasive population in Alligator creek near Townsville, Australia (49,50). Since 2019 these stocks have been kept in mixed-sex tanks (~50 fish per 60L aquaria) in controlled temperature rooms at 26 ± 1 °C with a 14:10 light/dark cycle and fed twice daily with live brine shrimp nauplii (*Artemia sp.*) and fish flakes (Aqua one). To start our experiment, we collected newborn fry and transferred them into 7L plastic tanks (up to 10 fry/tank). Juveniles were then inspected weekly to determine their sex. Immature males and females were transferred to single-sex aquaria to ensure their virginity as adults.

Experimental protocol

To generate test fish, we randomly paired a virgin male and virgin female in an individual 7L tank (n = 28 pairs), under the same conditions as stock fish. After two weeks, we removed the males and then inspected tanks daily for newborn fry. On the day of birth (Day 0), we transferred each offspring to its own 1L tank. Newborn fry within each brood were alternately assigned to our four experimental treatments: control temperature/control diet; control temperature/restricted diet; high temperature/control diet; high temperature/restricted diet.

We manipulated temperature by placing tanks in temperature-controlled rooms at either 26 ± 1 °C (control) or 30 ± 1 °C (high) on Day 0. This equated to water temperatures of 24.4 ± 0.6 °C (control) and 27.8 ± 0.4 °C (high). Water temperature in guppies' native habitat ranges from 20-28°C (51), but the upper value is predicted to increase as global temperatures rise (52,53). Fish remained in their temperature treatment throughout the experiment. Newborn fry were fed *ad libitum* with brine shrimp nauplii for three days (Days 0-2) and then began their diet treatment on Day 3. Fry on the control diet were fed brine shrimp nauplii *ad libitum* (approximately 6 mg) twice daily, whereas fry on the restricted diet were fed 3 mg of brine shrimp once a day every second day for 14 days (i.e., 12.5% of control diet until day 17). This feeding regime led to near zero growth without elevated mortality in another poecilid fish (48). On Day 17, all fish were returned to the control diet. In total, we used offspring from 28 pairs to set up 110 fish per treatment (total N = 440).

To measure growth, we photographed fish on Day 3 (prior to diet restriction), Day 17 (at the end of diet restriction) and Day 31 (two weeks after a return to the control diet). We placed each fry in a small container of shallow water containing a 1 cm ruler and then photographed it from above using a digital camera (Canon PowerShot SX620 HS). Standard length (tip of the snout to the end of the caudal peduncle) was later measured using *ImageJ* software (54).

We inspected fish twice a week from Day 31 to determine the time to sexual maturity. We considered females to be sexually mature when we observed a visible egg spot near their rounded anal fin and males to be mature when we observed a fully-developed hood and hooks at the tip of their gonopodium (47,55). On the day of maturity, we anaesthetised each fish using AQUI-S (New Zealand; 20 mg/L) for 30 seconds, placed it on its side on a glass slide, and photographed it next to a scaled ruler. Standard length was again measured using *ImageJ*.

We calculated the instantaneous rate of growth for three periods: (1) Day 3 to 17 (diet restriction); (2) Day 17 to 31; and (3) from the end of the diet restriction to sexual maturity (from Day 3 for fish on the control diet; from Day 17 for fish on the restricted diet). We used the formula:

$$G = \frac{ln\ (\frac{Lt1}{Lt0})}{t}$$

where *Lt0* and *Lt1* is length on the initial and final day of the focal period, respectively, and *t* is the duration of the period (in days) (48). We used *initial* growth to determine whether there is compensatory growth. *Initial growth* refers to the period immediately after the diet restriction ended. This allows for a direct comparison across treatments for fish that were initially the same size. In a previous study, Vega-Trejo et al (48) showed that the diet restriction treatment we used resulted in minimal growth such that Day 3 fish on the control diet and Day 17 fish on the restricted diet were almost identical in size. Indeed, in our study, body size was similar for restricted diet (day 17) and control diet fish (day 3) at the control temperature (control diet: mean (± SD): 11.40 ± 0.85 mm; restricted diet: mean (± SD): 11.61 ± 0.75 mm) and the high temperature (control diet: mean (± SD): 12.46 ± 0.93 mm; restricted diet: mean (± SD): 12.38 ± 0.84 mm). To test for compensatory growth, we therefore tested whether growth from day 17-31 for fish on the restricted diet differed from growth from day 3-17 for fish on the control diet. In addition, we quantified *overall* growth, which was defined as growth from the end of diet restriction (or its equivalent) until sexual maturity (i.e., starting at day 3 for control fish and day 17 for diet restricted fish). The mean duration of the growth period varied among the four treatments because the treatments affected the time to sexual maturation (see Results). Because the duration over which growth was measured differs among fish, it is more difficult to determine whether there is compensatory growth, because growth rates change with size, hence age.

Statistical analyses

The effects of temperature and diet restriction on our five focal traits (body size on Day 17; initial growth rate; overall growth rate; size at maturity; age at maturity) were analysed using individual linear mixed models (LMM) in the ‘lmer’ function of the ‘lme4’ package in R version 4.2.2 (56). To test whether fish exhibited compensatory growth in response to a restricted diet early in life, and whether compensatory growth was affected by temperature, we included early life diet (control or restricted), temperature (control or high) and their interaction as fixed effects in our models. Additionally, we included sex (male or female) and all possible two- and three-way interactions involving sex in our models. Brood identity was included as a random factor to account for measurement of several offspring from the same family. We used histograms and Q-Q plots to confirm that model residuals met assumptions of normality.

We removed any non-significant higher order interactions to interpret lower order interactions and/or main effects (57). If our analysis revealed a significant three-way or two-way interaction involving sex, we ran separate analyses for each sex. If there was a significant interaction between diet and temperature, we conducted Tukey’s post-hoc pairwise comparisons (‘emmeans’ function of the ‘emmeans’ package) between the four treatment groups.

We used the ‘Anova’ function of the ‘car’ package (type III Wald chi-square or F-tests) to determine the p-value (alpha = 0.05; two-tailed). We pre-registered all statistical analyses with the Open Science Framework, and any deviations from our analyses are detailed in the supplementary material.

Results

The full and reduced models and all Tukey's post-hoc pairwise comparisons are available in the supplementary materials (Supplementary Tables 1-16).

Body size after the period of diet restriction

There was no effect of sex on body size on Day 17 (sex: χ^2 =0.959, p = 0.327; sex*diet: χ^2 = 0.416, p = 0.519; sex*temp: χ^2 = 0.298, p = 0.585). Diet and temperature interacted to affect body size at the end of the diet treatment on Day 17 (χ^2 = 99.858, p < 0.001). Control fish were 3.6 mm larger than diet restricted fish at the control temperature (Tukey's test, p < 0.001), and 4.8 mm larger at the high temperature (Tukey's test, p <0.001). Fish on the control diet reached a significantly larger size on Day 17 when they were at the higher temperature (Tukey's test, p < 0.001). Fish on a restricted did not differ in body size at the high or control temperature (Tukey's test, p = 0.342).

Initial growth

Sex had no effect on initial growth (three-way interaction: χ^2 = 0.869, p = 0.351; sex*diet: χ^2 = 0.900, p = 0.340; sex*temp: χ^2 = 1.840, p = 0.170; sex: χ^2 = 0.715, p = 0.398; Supplementary Table 3). Diet and temperature did not interact to affect initial growth (χ^2 = 0.900, p = 0.340; Fig 1). However, both diet and temperature independently affected initial growth. Immediately after the diet restriction period, fish on the restricted diet grew significantly faster for the next two weeks than initially similar-sized fish on the control diet (χ^2 = 87.452, p < 0.001). There is therefore compensatory growth. Fish grew significantly faster at the high than the control temperature (χ^2 = 119.213, p < 0.001).

Overall growth

Diet, temperature, and sex interacted to affect overall growth (χ^2 = 5.919, p = 0.015). We therefore analysed each sex separately.

For females there was a strong effect of diet on overall growth (χ^2 = 75.125, p < 0.001), with a weak interaction between diet and temperature (χ^2 = 4.195, p = 0.041). The strong effect of diet on overall growth meant that females that were initially on the restricted diet had greater overall growth than females that were on the control diet (Fig 2a). The weak interaction occurred because the difference in growth between the diets was slightly smaller for the high than control temperature. It should be noted, however, that the effect of temperature was not significant for fish on either the control or restricted diet (Tukey's test, p = 0.301 and p = 0.659, respectively), which is why we report the main effect of diet.

For males there was no interaction between diet and temperature (χ^2 = 2.1821, p = 0.140). Diet restriction (χ^2 =72.0101, p < 0.001) and high temperature (χ^2 =79.9817, p < 0.001) both lead to a significant increase in the overall growth rate (Fig 2b).

Age at maturity

There was no significant three-way interaction between diet, temperature and sex (χ^2 = 2.918, p = 0.088), but there was an interaction between temperature and sex (χ^2 = 134.265, p < 0.001). We therefore analysed the sexes separately.

For females, diet and temperature interacted to affect age at maturity (χ^2 = 11.823, p < 0.001; Fig 2c). Females on the restricted diet matured significantly later at both the high and control temperatures (Tukey's test, p = 0.005 and p < 0.001 respectively), but the difference was much greater at the high temperature (4.9 days vs 12.4 days; Fig2c).

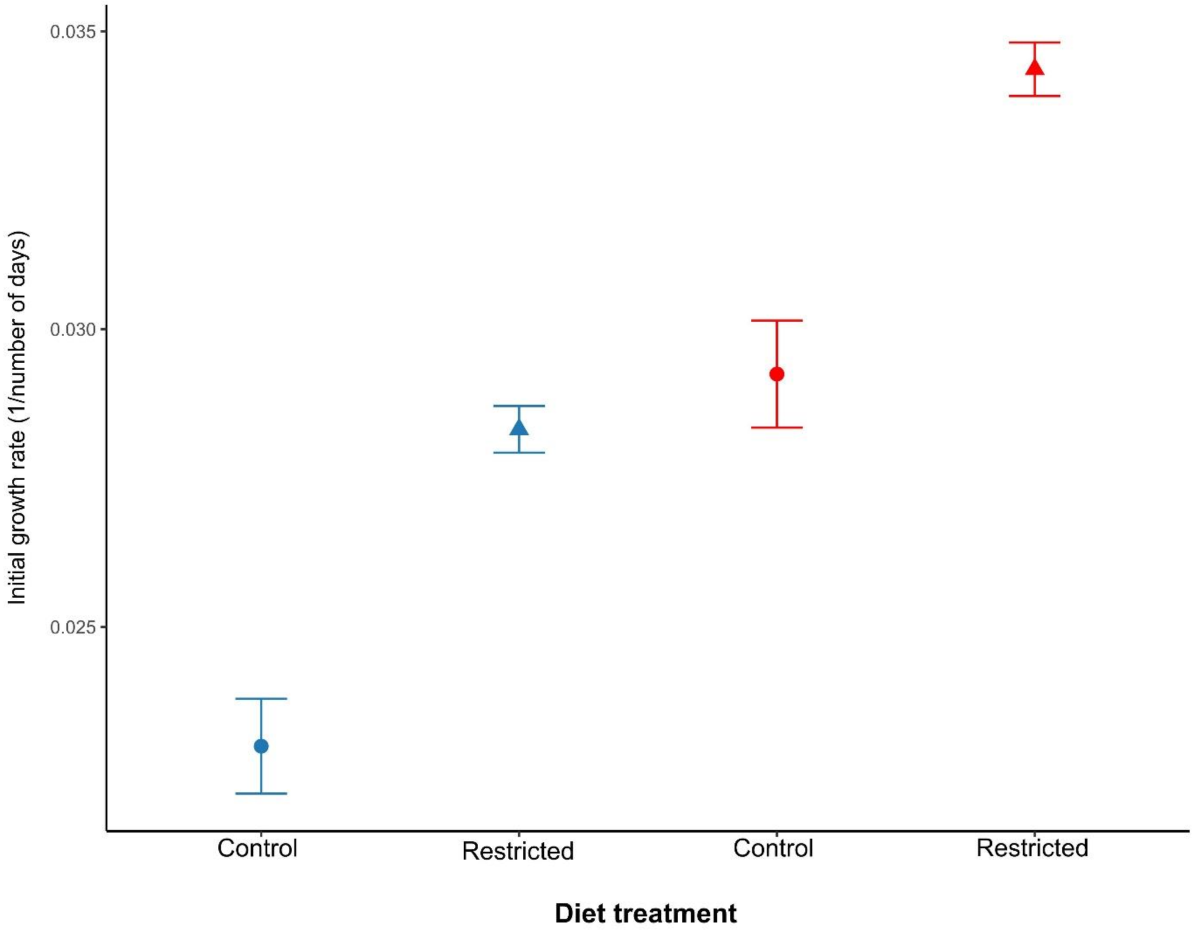
For males, diet and temperature weakly interacted to affect age at maturity ($\chi^2 = 29.595$, $p < 0.033$). At both the control and high temperature, males on the restricted diet matured significantly later than control fish, but the effect was slightly stronger at the high temperature (Tukey's tests, both $p < 0.001$; Fig 2d). Males also matured significantly sooner at the high temperature (Tukey's test, $p < 0.001$). The combined effect meant that the time to reach maturity for males on a restricted diet at the high temperature did not differ from males on the control diet at the control temperature (Tukey's test: $p = 0.108$; Fig 2d).

Size at maturity

Size at maturity was affected by a three-way interaction between diet, temperature, and sex ($\chi^2 = 5.389$, $p = 0.020$). We therefore analysed the sexes separately.

For females there was a significant interaction between diet and temperature that affected size at maturity ($\chi^2 = 9.108$, $p = 0.003$). At the control temperature, females on the restricted diet matured at a smaller size than those on the control diet (Tukey's test, $p = < 0.001$; Fig 2e). But at the high temperature, females on the restricted and control diet matured at the same size (Tukey's test, $p = 0.989$; Fig 2e).

For males there was no interaction between diet and temperature affecting size at maturity ($\chi^2 =0.246$, $p = 0.620$). There was also no effect of diet ($\chi^2 = 2.915$, $p = 0.088$; Fig 2f). However, males matured at a smaller size at the high than the control temperature ($\chi^2 = 13.878$, $p < 0.001$; Fig 2f).



254 Fig 1. Mean initial growth rates (G = (ln(Lt1/Lt0))/t) separated by treatment (diet *
255 temperature). The control temperature is represented in blue and the high temperature in
256 red. Circles represent the control diet and triangles the restricted diet during early life. Error
257 bars are standard errors.

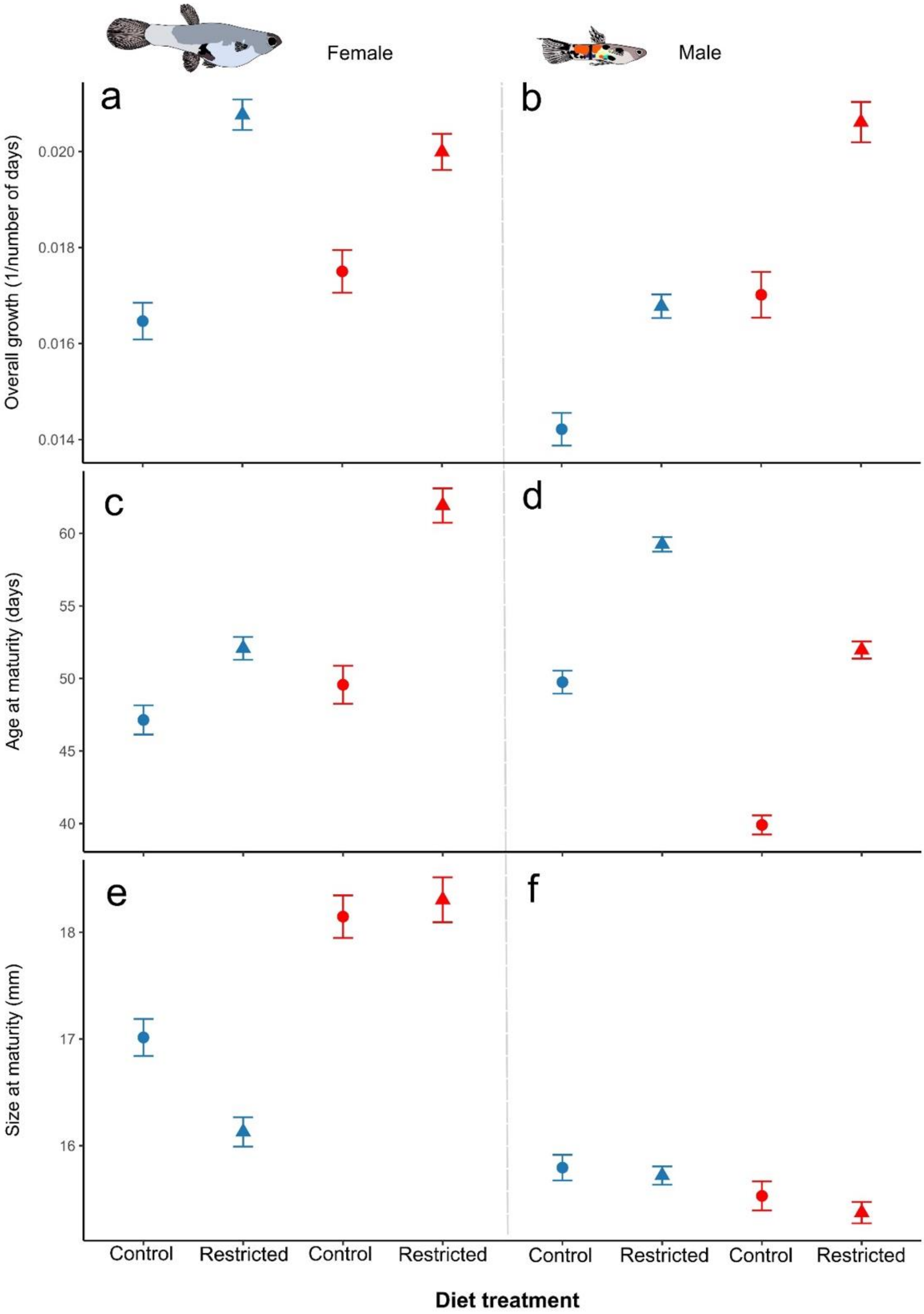


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Fig 2. Mean overall growth rates ($G = (\ln(Lt1/Lt0))/t$; a,b), age at maturity (c,d) and size at maturity (e,f) separated by sex (females: left; males: right) and treatment (diet * temperature). The control temperature is represented in blue and the high temperature in red. Circles represent the control diet and triangles represent the restricted diet during early life. Error bars are standard errors.

Discussion

Compensatory growth allows animals to reduce costs associated with small adult size and/or delayed maturation that would otherwise result after periods of diet restriction during development. While compensatory growth is commonplace in many taxa (9), little is known about how environmental factors shape this diet-mediated growth response. We investigated whether a higher temperature reduces an individual's ability to accelerate growth after a period of diet restriction that slowed its development. We found that the initial growth of guppies immediately after experiencing a restricted early-life diet was faster than that of fish on a constant control diet. There was clear evidence for compensatory growth at both the control and high temperature. This did not support our prediction that compensatory growth would not occur at the higher temperature (see Prediction 1). A higher temperature did, however, alter the age and size at which guppies reached maturity, but did so differently for males and females. The response of males to the diet and temperature treatments supported two of our three predictions about time to maturity and size at maturity (Predictions 2-3; but not Prediction 4). In contrast, the response of females to diet and temperature treatments did not support our predictions about time to maturity and size at maturity (except for the time to maturity on the restricted diet). Our results highlight the need to test for sex differences when evaluating how temperature affects key life history traits.

Guppies show compensatory growth even at higher temperatures

At the control temperature males and females showed a faster initial growth rate after a period of diet restriction than those on the control diet (i.e. compensatory growth). Contrary to our predictions, however, high temperature did not prevent guppies from increasing their initial or overall growth after diet restriction. This highlights that guppies exhibit compensatory growth immediately after diet restriction period and maintain higher growth until sexual maturity. This faster growth occurred even at a higher temperature where energetic demands are higher (18). Interestingly, absolute growth was greater at the higher temperature. This highlights that even when there is compensatory growth at the control temperature, guppies were not growing at their maximum rate. Under natural conditions there may be selection against maximising growth either because of immediate ecological costs, such as predation associated with foraging, or because of hidden fitness costs that arise later in life (58). Our results suggest that selection on growth changes with temperature since a higher temperature increased growth rates, which – all else being equal – should increase ecological and/or physiological costs. Our experimental design allowed animals to acclimate to high temperatures from birth, which might lower the short-term physiological costs of generating reactive oxygen species during growth (18). This could explain how guppies could sustain faster growth at high temperatures. Future research should explore how fluctuating temperatures affect compensatory growth since continued acclimatization to new temperatures is expected to impose high physiological costs on ectotherms (18), potentially hindering growth.

Sex differences in developmental patterns

At both temperatures, males showed full compensatory growth because those initially on a restricted diet reached maturity at the same size as their well-fed counterparts. However, overall males reached maturity at a smaller size at the higher temperature compared to the control temperature. In contrast, females showed full compensatory growth at the high temperature, but only partial compensatory growth at the control temperature. Females that were initially on a restricted diet reached maturity at the same size as their well-fed counterparts at the high temperature, but at a significantly smaller size than their well-fed counterparts at the control temperature. These results broadly corroborate previous research on guppies showing full compensatory growth by males (47) and partial compensatory growth by females (45).

Prey availability, population density and predation pressure all vary in freshwater ecosystems (59–61) causing variation in food acquisition by guppies (62). It is likely that compensatory growth under natural conditions allows guppies to compensate for slower early growth and improve adult fitness (45). Compensatory growth is expected when there is strong selection for larger adults, either because size increases survival (63) or reproductive success (64,65). In guppies, both sexes prefer larger mates (66,67). Larger males also obtain advantages during male-male contests (68,69); while larger females are more fecund (65,66,70). Thus, both sexes appear to benefit from being larger. The sexes differ, however, in that males barely grow after they reach sexual maturity (71), while females continue to grow as adults. Consequently, there may be stronger selection on males against maturing at a smaller size. Why then do females show compensatory growth if there are potential long-term costs? One possibility is that once females start to reproduce, those that failed to show compensatory growth after being on a restricted diet would never match the fecundity of their well-fed counterparts. Alternatively, faster juvenile growth could be a byproduct of the greater foraging effort that is commonly seen in fishes after dietary restriction ends (10,28). Increased foraging after food deprivation may have evolved to avoid starvation in environments with fluctuating food availability rather than for benefits associated with faster growth.

Developmental patterns will be modified as temperatures rise

Although the high temperature did not prevent compensatory growth, it had opposing effects on male and female development. Males matured at a smaller size at the high than control temperature, regardless of their diet. In contrast, females matured at a *larger* size at the high than control temperature, albeit with the effect being stronger for females on the restricted diet (Fig 2e,f). Faster development at higher temperatures is widely attributed to temperature elevating metabolic rates (21,72), which implies that both sexes will respond similarly to rising temperatures. It is, however, plausible that the sexes respond differently because males and females optimise their life-histories in different ways (73,74). Larger females benefit by producing more eggs (65,66,70), while males might gain a net benefit by offsetting costs of being smaller adults (67,75) against the benefit that maturing sooner prolongs access to females (7,21). Controlling for other factors, time to and size at maturity are usually negatively related in poecilids (45,48,76) . Intriguingly, the sexes differed in how treatment differences in the size at maturity were mediated by the time taken to reach maturity. Controlling for diet, at the higher temperature males grew faster and reached maturity sooner. In contrast, at the higher temperature females on the restricted diet took far longer to reach maturity than females on the control diet but still ended up at the same size at maturity. This suggests that a restricted diet lowered the ability of females to grow after the initial phase of high compensatory growth.

We have discussed the effect of temperature on development assuming the observed responses are adaptive. It is, however, worth noting that temperature can set limits on biological functions and impose physiological constraints. The observed temperature-dependent changes in development might not be adaptive plastic responses (21). Our high temperature treatment was such that fish were closer to their upper thermal limit for an extended period, which is a situation outside the average historic conditions that guppies have experienced (51,77). The observed growth and maturation patterns might therefore reflect physiological constraints. For example, in fish high temperatures tend to increase feeding rates (27,78,79), and growth hormone production (80,81). Both these changes should accelerate growth and shorten the time to maturation. However, the sexes differed in their response to a higher temperature so additional factors are required to invoke a non-adaptive explanation. For example, there might be an interaction between higher growth hormone production at higher temperatures and sex-specific steroids causing sex differences in the time to, and size at, maturation (82–84).

Conclusions

A high temperature did not directly affect compensatory growth, but it changed development in a sex-specific manner: after diet restriction males matured smaller and sooner, while females matured later and larger than their counterparts on the control diet. Compensatory growth is viewed as an adaptive response to a temporary reduction in food availability during development (85), but studies have shown that faster growth can have long-term fitness costs (e.g. 28,30,85). Given that we found that the higher temperature increased growth rates and modified developmental patterns, rising temperatures could exacerbate existing fitness costs of compensatory growth reported for guppies (44). Future studies should investigate if early-life diet restriction at higher temperatures is associated with a greater decline in fecundity, which could lower population growth or the likelihood of persistence. Temperature is predicted to rise, and food availability to become more variable, making it more important to understand their combined effects. This is especially the case for tropical fishes, like guppies, that are sensitive to temperature changes due to their lower thermal range and more complex trophic interactions (37,38).

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Supplementary materials

Supplementary methods

Statistical analysis

We have pre-registered our statistical analyses following the Open Science Framework. We have included another growth rate variable that was not present in our original analyses. For that, we calculated growth rate until sexual maturity for all treatments to better understand overall compensatory growth, following (Vega-Trejo et al., 2016). Additionally, we originally described performing model analysis including all three-way interactions (diet, temperature, and sex). Since we obtained multiple two and three-way interactions for several of our models and given the biological differences between male and female guppies, we extended our original analyses by splitting our models for three variables (overall growth rate, age, and size at maturity) by sex to better understand the sex specific effects.

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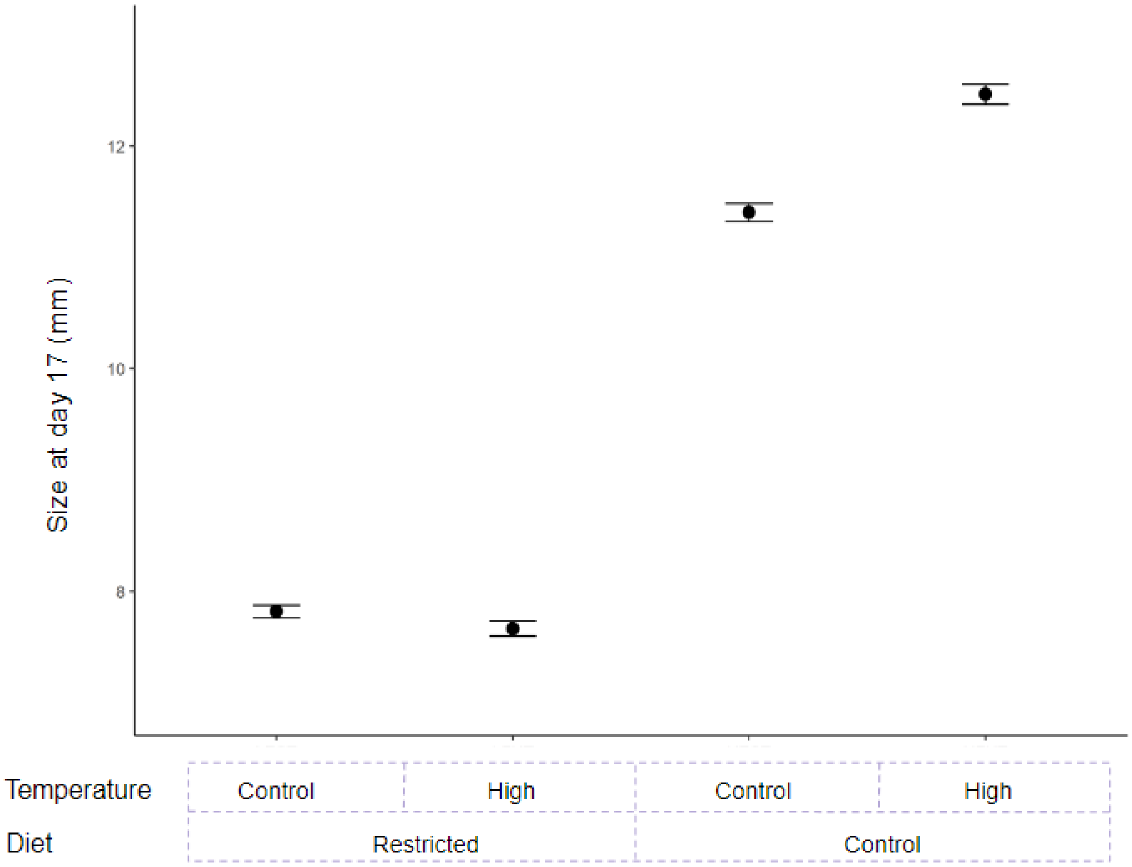
Supplementary figures



Supplementary Fig 1. Mean body size immediately after diet restriction period (day 17) separated by treatment (diet * temperature). Error bars are standard errors.

Supplementary Table 1. Results from linear mixed models (LMM) of body size at day 17 (after diet restriction period) with chi-square (χ2) values for significance tests of estimated parameters for diet, temperature, and sex.

Full model	**Estimate**	***SE***	***df***	**χ^2**	***P***
Fixed effects					
Intercept (control, control, female)	11.425	0.120	82.368	9034.556	< 0.001
Diet (restricted)	-3.521	0.122	395.558	830.115	< 0.001
Temperature (high)	1.114	0.121	397.550	84.018	< 0.001
Sex (male)	-0.004	0.124	398.162	0.001	0.974
Diet * Temp	-1.226	0.175	397.173	49.208	< 0.001
Diet * Sex	-0.086	0.176	399.030	0.238	0.625
Temp * Sex	-0.074	0.179	401.508	0.168	0.682
Diet * Temp * Sex	0.010	0.253	400.973	0.001	0.970

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	0.1889	0.4346	28

Two-way model	**Estimate**	***SE***	***Df***	**χ^2**	***P***
Fixed effects					
Intercept (control, control, female)	11.426	0.117	74.130	9574.518	**< 0.001**
Diet (restricted)	-3.523	0.105	396.187	1109.192	**< 0.001**
Temperature (high)	1.111	0.104	396.928	112.039	**< 0.001**
Sex (male)	-0.006	0.107	399.779	3.6e-3	0.952
Temp * Sex	-0.688	0.125	400.912	0.298	0.585
Diet * Sex	-0.081	0.125	401.5	0.416	0.519
Diet * Temp	-1.221	0.122	394.401	99.858	**< 0.001**

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	0.1889	0.4346	28

Reduced model	**Estimate**	***SE***	***Df***	**χ^2**	***P***
Fixed effects					

Intercept (control, control, female)	11.76	0.11	55.17	11592.93	**< 0.001**
Diet (restricted)	-4.16	0.07	399.75	3707.26	**< 0.001**
Temperature (high)	0.47	0.07	398.19	47.71	**< 0.001**
Sex (male)	-0.07	0.07	404.56	0.959	0.327

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	0.186	0.4312	28

Supplementary Table 2. Results from estimated marginal means (EEMs) pairwise comparisons among four treatments for body size at day 17 (after diet restriction period) with t-ratio values for significance tests.

Contrast	**t ratio**	**p value**
Control diet, control temp - Restricted diet, control temp	41.589	**< 0.001**
Control diet, control temp - Control diet, high temp	-12.493	**< 0.001**
Control diet, control temp - Restricted diet, high temp	42.542	**< 0.001**
Restricted diet, control temp - Control diet, high temp	-53.937	**< 0.001**
Restricted diet, control temp - Restricted diet, high temp	1.667	0.342
Control diet, high temp - Restricted diet, high temp	54.724	**< 0.001**

Supplementary Table 3. Results from linear mixed models (LMM) of initial growth rate with chi-square ($\chi2$) values for significance tests of estimated parameters for diet, temperature, and sex.

Full model	**Estimate**	***SE***	***df***	χ^2	***P***
Fixed effects					
Intercept (control, control, female)	0.022	0.001	89.199	425.125	< 0.001
Diet (restricted)	0.006	0.001	387.933	32.197	< 0.001
Temperature (high)	0.008	0.001	389.022	43.627	< 0.001
Sex (male)	0.001	0.001	391.069	1.371	0.242
Diet * Temp	-0.001	0.002	388.874	0.493	0.482
Diet * Sex	-0.002	0.002	392.199	1.772	0.183
Temp * Sex	-0.003	0.002	394.563	2.607	0.106
Diet * Temp * Sex	0.002	0.002	393.892	0.869	0.351

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	1.274e-05	0.003	28

Two-way interaction model	Estimate	*SE*	*df*	χ^2	*P*
Fixed effects					
Intercept (control, control, female)	0.022	0.001	79.753	461.460	< 0.001
Diet (restricted)	0.006	0.001	388.336	36.010	< 0.001
Temperature (high)	0.007	0.001	388.861	50.590	< 0.001
Sex (male)	0.001	0.001	392.566	0.670	0.410
Diet * Sex	-0.001	0.001	394.390	0.900	0.340

Temp * Sex	-0.002	0.001	394.466	1.840	0.170
Diet * Temp	-5.8e-05	0.001	385.971	0.000	0.960

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	1.281e-05	0.003	28

Reduced model	**Estimate**	***SE***	***df***	**χ^2**	***P***
Fixed effects					
Intercept (control, control, female)	0.023	9.118e-04	51.251	615.658	< **0.001**
Diet (restricted)	0.005	5.713e-04	390.951	87.452	< **0.001**
Temperature (high)	0.006	5.711e-04	389.373	119.213	< **0.001**
Sex (male)	-4.942e-4	5.843e-04	396.244	0.715	0.398

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	1.297e-05	3.601e-3	28

Supplementary Table 4. Results from linear mixed models (LMM) of overall growth rate with chi-square (χ2) values for significance tests of estimated parameters for diet, temperature, and sex. Given a significant three-way interaction, we followed this up by running separate models for males and females to look at sex specific effects (see Supplementary Tables 5 and 7).

Full model	**Estimate**	***SE***	***df***	**χ^2**	***P***
Fixed effects					
Intercept (control, control, female)	0.016	0.000	131.059	1689.546	< 0.001
Diet (restricted)	0.004	0.000	389.137	76.487	< **0.001**
Temperature (high)	0.001	0.000	391.428	4.317	**0.038**
Sex (male)	-0.002	0.000	393.368	25.195	< **0.001**
Diet * Temp	-0.002	0.001	390.577	5.423	**0.020**
Diet * Sex	-0.001	0.001	394.761	4.619	**0.032**
Temp * Sex	0.002	0.001	398.156	6.761	**0.009**
Diet * Temp * Sex	0.002	0.001	396.665	5.919	**0.015**

Random effect	**Variance**	***sd***	**Number of groups**

Brood ID (intercept)	1.255e-06	0.001	28

Supplementary Table 5. Results from linear mixed models (LMM) of overall female growth rate with chi-square (χ2) values for significance tests of estimated parameters for diet and temperature.

Full model	**Estimate**	***SE***	***df***	**χ^2**	***P***
Fixed effects					
Intercept (control, control)	0.017	4.213e-04	68.265	1536.714	< 0.001
Diet (restricted)	0.004	4.666e-04	190.928	75.125	**< 0.001**
Temperature (high)	0.001	4.758e-04	192.370	3.080	0.079
Diet * Temp	-0.001	6.822e-04	191.542	4.195	**0.041**

Random eff	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	1.766e-06	0.001	28

Supplementary Table 6. Results from estimated marginal means (EEMs) pairwise comparisons among four treatments (diet * temperature) for overall female growth rate with t-ratio values for significance tests.

Pairwise comparison	**t ratio**	**p value**
Control diet, control temp - Restricted diet, control temp	-8.65	**< 0.001**
Control diet, control temp - Control diet, high temp	-1.751	0.301
Control diet, control temp - Restricted diet, high temp	-7.263	**< 0.001**
Restricted diet, control temp - Control diet, high temp	6.646	**< 0.001**
Restricted diet, control temp - Restricted diet, high temp	1.15	0.659
Control diet, high temp - Restricted diet, high temp	-5.345	**< 0.001**

Supplementary Table 7. Results from linear mixed models (LMM) of overall male growth rate with chi-square (χ2) values for significance tests of estimated parameters for diet and temperature.

Full model	**Estimate**	***SE***	***df***	**χ^2**	***P***

Fixed effects					
Intercept (control, control)	0.014	4.142e-04	87.885	1158.130	< 0.001
Diet (restricted)	0.003	4.898e-04	186.770	26.462	< 0.001
Temperature (high)	0.003	5.137e-04	191.652	26.399	< 0.001
Diet * Temp	0.001	7.104e-04	188.155	2.182	0.140

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	1.103e-06	0.001	28

Reduced model	**Estimate**	***SE***	***df***	χ^2	***P***
Fixed effects					
Intercept (control, control)	0.014	3.719e-04	65.24	1382.316	< 0.001
Diet (restricted)	0.003	3.557e-04	189.9	72.010	< **0.001**
Temperature (high)	0.003	3.565e-04	190.6	79.982	< **0.001**

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	1.086e-06	0.001	28

Supplementary Table 8. Results from linear mixed models (LMM) of age at maturity with chi-square (χ2) values for significance tests of estimated parameters for diet, temperature, and sex. Given multiple two-way interactions, we followed this up by running separate models for males and females to look at sex specific effects (see Supplementary table 9 and 10).

Full model	**Estimate**	***SE***	***df***	χ^2	***P***
Fixed effects					
Intercept (control, control, female)	46.832	0.916	231.241	2611.571	< **0.001**
Diet (restricted)	5.104	1.222	406.064	17.437	< **0.001**
Temperature (high)	2.473	1.212	410.701	4.161	**0.041**
Sex (male)	2.922	1.237	410.853	5.580	**0.018**
Diet * Temp	7.215	1.748	409.379	17.034	< **0.001**
Diet * Sex	4.107	1.751	412.383	5.500	0.019
Temp * Sex	-12.431	1.780	416.391	48.751	< **0.001**

Diet * Temp * Sex	-4.306	2.521	415.190	2.918	0.088

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	3.055	1.748	28

Two-way model	**Estimate**	***SE***	***Df***	**χ^2**	***P***
Fixed effects					
Intercept (control, control, female)	46.349	0.876	203.246	2799.764	< **0.001**
Diet (restricted)	6.140	1.064	405.370	33.312	< **0.001**
Temperature (high)	3.497	1.055	407.369	10.982	**0.001**
Sex (male)	3.974	1.076	411.618	13.643	< **0.001**
Diet * Temp	5.100	1.236	400.699	17.028	**< 0.001**
Diet * Sex	2.017	1.257	414.764	2.576	0.109
Temp * Sex	-14.587	1.259	415.115	134.265	**< 0.001**

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	3.156	1.777	28

Supplementary Table 9. Results from linear mixed models (LMM) of female age at maturity with chi-square (χ2) values for significance tests of estimated parameters for diet, temperature, and sex.

Full model	**Estimate**	***SE***	***df***	**χ^2**	***P***
Fixed effects					
Intercept (control, control, female)	46.839	1.145	106.537	1673.010	< 0.001
Diet (restricted)	4.970	1.472	204.291	11.406	**< 0.001**
Temperature (high)	2.352	1.464	207.911	2.580	0.108
Diet * Temp	7.258	2.111	206.868	11.823	**< 0.001**

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	6.457	2.541	28

Reduced model	Estimate	*SE*	*df*	χ^2	*P*
Fixed effects					
Intercept (control, control, female)	45.192	1.061	83.114	1812.597	< 0.001
Diet (restricted)	8.524	1.075	206.317	62.852	**< 0.001**

Temperature (high)	5.860	1.077	207.670	29.595	< **0.001**

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	6.557	2.561	28

Supplementary Table 10. Results from estimated marginal means (EEMs) pairwise comparisons among four treatments (diet * temperature) for female age at maturity with t-ratio values for significance tests.

Contrast	**t ratio**	**p value**
Control diet, control temp - Restricted diet, control temp	-3.368	**0.005**
Control diet, control temp - Control diet, high temp	-1.599	0.382
Control diet, control temp - Restricted diet, high temp	-9.813	< **0.001**
Restricted diet, control temp - Control diet, high temp	1.754	0.299
Restricted diet, control temp - Restricted diet, high temp	-6.328	< **0.001**
Control diet, high temp - Restricted diet, high temp	-8.096	< **0.001**

Supplementary Table 11. Results from linear mixed models (LMM) of male age at maturity with chi-square (χ2) values for significance tests of estimated parameters for diet, temperature, and sex.

Full model	**Estimate**	***SE***	***df***	χ^2	***P***
Fixed effects					
Intercept (control, control, female)	49.830	0.666	129.749	5597.141	< 0.001
Diet (restricted)	9.335	0.881	197.898	112.145	< **0.001**
Temperature (high)	-9.963	0.910	202.770	119.925	< **0.001**
Diet * Temp	2.713	1.269	200.280	4.568	**0.033**

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	0.764	0.874	28

Supplementary Table 12. Results from estimated marginal means (EEMs) pairwise comparisons among four treatments (diet * temperature) for male age at maturity with t-ratio values for significance tests.

Contrast	**t ratio**	**p value**
Control diet, control temp - Restricted diet, control temp	-10.541	**< 0.001**
Control diet, control temp - Control diet, high temp	10.869	**< 0.001**
Control diet, control temp - Restricted diet, high temp	-2.272	0.108
Restricted diet, control temp - Control diet, high temp	21.772	**< 0.001**
Restricted diet, control temp - Restricted diet, high temp	8.153	**< 0.001**
Control diet, high temp - Restricted diet, high temp	-13.117	**< 0.001**

Supplementary Table 13. Results from linear mixed models (LMM) of size at maturity with chi-square ($\chi 2$) values for significance tests of estimated parameters for diet, temperature, and sex. Given the three-way interaction, this model was divided for males and females (see Supplementary Table 14 and 16).

Full model	**Estimate**	***SE***	***df***	**χ^2**	***P***
Fixed effects					
Intercept (control, control, female)	17.021	0.167	99.591	10338.480	< 0.001
Diet (restricted)	-0.839	0.183	394.725	21.008	**< 0.001**
Temperature (high)	1.195	0.182	397.620	43.103	**< 0.001**
Sex (male)	-1.244	0.186	397.985	44.811	**< 0.001**
Diet * Temp	0.930	0.264	396.746	12.384	**< 0.001**
Diet * Sex	0.720	0.263	398.994	7.467	**0.006**
Temp * Sex	-1.517	0.269	402.115	31.797	**< 0.001**
Diet * Temp * Sex	-0.886	0.382	401.144	5.389	**0.020**

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	0.309	0.556	28

Supplementary Table 14. Results from linear mixed models (LMM) of female size at maturity with chi-square ($\chi 2$) values for significance tests of estimated parameters for diet, temperature, and sex.

Full model	**Estimate**	***SE***	***df***	**χ^2**	***P***
Fixed effects					

Intercept (control, control, female)	17.008	0.206	64.233	6798.934	< 0.001
Diet (restricted)	-0.904	0.224	194.555	16.330	< 0.001
Temperature (high)	1.143	0.224	197.347	26.121	< 0.001
Diet * Temp	0.979	0.324	196.164	9.108	**0.002**

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	0.451	0.671	28

Supplementary Table 12. Results from estimated marginal means (EEMs) pairwise comparisons among four treatments (diet * temperature) for female size at maturity with t-ratio values for significance tests.

Contrast	**t ratio**	**p value**
Control diet, control temp - Restricted diet, control temp	4.034	**< 0.001**
Control diet, control temp - Control diet, high temp	-5.097	**< 0.001**
Control diet, control temp - Restricted diet, high temp	-5.296	**< 0.001**
Restricted diet, control temp - Control diet, high temp	-9.031	**< 0.001**
Restricted diet, control temp - Restricted diet, high temp	-9.047	**< 0.001**
Control diet, high temp - Restricted diet, high temp	-0.32	0.989

Supplementary Table 16. Results from linear mixed models (LMM) of male size at maturity with chi-square (χ2) values for significance tests of estimated parameters for diet, temperature, and sex.

Full model	**Estimate**	***SE***	***df***	**χ^2**	***P***
Fixed effects					
Intercept (control, control, female)	15.875	0.137	58.028	13460.200	< 0.001
Diet (restricted)	-0.202	0.128	184.497	2.480	0.115
Temperature (high)	-0.392	0.134	187.031	8.623	0.003
Diet * Temp	0.092	0.185	185.002	0.246	0.620

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	0.264	0.513	28

Reduced model	**Estimate**	***SE***	***df***	**χ^2**	***P***
Fixed effects					
Intercept (control, control, female)	15.851	0.128	46.280	15431.040	< 0.001
Diet (restricted)	-0.157	0.092	186.711	2.915	0.088
Temperature (high)	-0.344	0.092	186.843	13.878	**< 0.001**

Random effect	**Variance**	***sd***	**Number of groups**
Brood ID (intercept)	0.261	0.511	28