

Distinct impacts of food restriction and warming on life history traits affect population fitness in vertebrate ectotherms

Abstract

Observed body size shifts in ectotherms are mostly attributed to the temperature size rule (TSR) stating that warming speeds up initial growth rate but leads to smaller size when food availability does not limit growth. However, climate warming can decrease food availability and we have limited information on how temperature and food jointly influence life history traits and population fitness. We investigated under laboratory conditions the independent and interactive effects of temperature (20 °C and 30 °C) and food availability (restricted or *ad libitum*) on the growth, fecundity and survival of the medaka fish *Oryzias latipes*. We next used our empirical estimates of vital rates as input parameters of an Integral Projection model (IPM) to predict how modifications in vital rates translate into population demographic parameters. Warming leads to a higher initial growth rate and lower size leading to crossed growth curves between the two temperatures. Food-restricted fish were smaller than *ad libitum* fed fish throughout the experiment, leading to nested growth curves. Fish reared at 30 °C matured younger, had smaller size at maturity, had a higher fecundity but had a shorter life span than fish reared at 20 °C. Food restriction increased survival probabilities under both temperature conditions. According to the IPM, warming reduces generation time and increases mean fitness in comparison to the cold treatments. Food restriction increased generation time and fitness in the cold treatment but had no effect in the warm treatment. Our results show that temperature and food interact on vital rates and population demographics. This is important in the context of global warming, as resources are expected to change with increasing temperatures.

Key-words: climate change, food restriction, temperature size rule, life-history traits, fish,

Integral Projection Model

24 Introduction

25 Body size reduction has been proposed as a third universal species response to global warming
 26 (Daufresne *et al.* 2009, Gardner *et al.* 2011, Sheridan and Bickford 2011), in addition to changes in
 27 phenology (Visser and Both 2005) and geographic distribution (Parmesan and Yohe 2003). While the
 28 first two responses have been studied extensively (Meyer *et al.* 1999), the third one has received less
 29 attention despite its high prevalence and magnitude. For instance, body size can reduce up to -4 %
 30 per °C in terrestrial species and up to -8 % per °C in aquatic ectotherms (Forster *et al.* 2012). Previous
 31 studies focused on proximal mechanisms, (i.e. how environmental factors influence life history traits
 32 by impacting physiological and developmental processes (Thierry 2005)) and ultimate mechanisms
 33 related to the evolution and adaptive value of body size changes (Atkinson and Sibly 1997, Frazier *et al.*
 34 *al.* 2001, Hoefnagel and Verberk 2015, Verberk *et al.* 2021, Walczyńska *et al.* 2015, Zuo *et al.* 2012)
 35 and their variability among species and habitats (Atkinson 1994, Forster *et al.* 2012, Horne *et al.* 2015).
 36 In aquatic systems, warming decreases oxygen concentration and hypoxia tends to amplify TS
 37 responses, which has been interpreted as a response to limited oxygen resource (Frazier *et al.* 2001,
 38 Hoefnagel and Verberk 2015, Verberk *et al.* 2021). In contrast, in terrestrial system, oxygen is less
 39 limiting and other factors may be more important than oxygen concentration. For instance, the risks
 40 of not completing juvenile development in time before the onset of winter strongly determine growth
 41 pattern in terrestrial organisms whereas it has less influence in the growth of aquatic organisms
 42 (Verberk *et al.* 2021). These differences may explain why TS responses are weaker in terrestrial than
 43 in aquatic ecosystems (Forster *et al.* 2012). At the individual level, body size shift can be explained by
 44 the "Temperature Size Rule" (TSR, Angilletta *et al.* 2004, Arendt 2007, Arendt 2011, Atkinson 1994,
 45 Atkinson and Sibly 1997, Berrigan and Charnov 1994, Perrin 1995), which states that ectotherms grow
 46 faster but reach a smaller size at a given stage of development (e.g. size at maturity or adult size) under
 47 warm environment compared to colder ones, resulting in "crossed" growth curves (Figure 1). This
 48 pattern of TSR remains an evolutionary puzzle (Atkinson and Sibly 1997) and body size shifts could be
 49 the result of different developmental strategies. For example, a recent study showed that warming

accelerates growth and reproduction leading to a rapid life cycle but also a decrease in adult survival in a temperate lizard species (Bestion *et al.* 2015). This study and others (Clissold and Simpson 2015, Corrêa *et al.* 2021, Courtney Jones *et al.* 2015, Kingsolver *et al.* 2006, Marn *et al.* 2017, Rohner *et al.* 2017) suggest that it is important to investigate the links between growth trajectories and fitness related traits (survival and fecundity) to better understand the underlying trade-offs and how the combination of these traits may influence individual fitness and population demographic parameters. However, most studies on TSR did not investigate these links (but see Corrêa *et al.* 2021, Kingsolver *et al.* 2006, Marn *et al.* 2017) which limits our ability to detect situations in which TSR might be adaptive (i.e. increase fitness) or maladaptive.

Besides temperature, another major factor underlying growth, reproduction and survival is food availability (Boggs and Ross 1993, Giberson and Rosenberg 1992, Boersma and Vijverberg 1996, Corrêa *et al.* 2021). Individuals need enough resources, as energy and material inputs, to sustain their metabolic demand and optimize the allocation of energy to growth, reproduction and maintenance (Lemoine and Burkepile 2012, Brown *et al.* 2004, Cross *et al.* 2015). There is a long history of researches on the influence of food availability on the growth rate and fecundity of ectothermic species (Rasmussen and Ostensfeld 2000, Johnston *et al.* 2002, Giberson and Rosenberg 1992, Boersma and Vijverberg 1996, Corrêa *et al.* 2021). In most cases, individuals with a higher food availability have a higher fecundity and have both a higher initial growth rate and a larger size at age compared to individuals under food restriction. In contrast to the pattern of crossed curves driven by temperature, different resource levels lead to a pattern of nested curves where the growth curve under limiting resources is nested below the growth curve under unlimited resources (Figure 1). Interestingly, food restriction may also be beneficial to the lifespan of organisms as this restriction reduces the production of senescence-accelerating oxidizing agents during metabolism (Sohal and Weindruch 1996, Gredilla *et al.* 2001, Speakman 2005), resulting in a “eat little die old” strategy. The effects of food restriction on fecundity (which decreases) and survival (which increases) are thus opposite and can be explained by a resources distribution to nutrient-limited processes (Corrêa *et al.* 2021). This indicates that we

should consider the effects of food restriction on multiple life history traits to better identify underlying trade-offs, fitness consequences and thus evolutionary strategies.

The interactive effects of temperature and food availability on life history traits have been studied in invertebrates such as daphnia (Betini *et al.* 2020, Giebelhausen and Lampert 2001, Wojewodzic *et al.* 2011, Persson *et al.* 2011), rotifers (Kielbasa *et al.* 2014), diatoms (Walczyńska and Sobczyk 2017), aquatic insect larvae (Giberson and Rosenberg 1992), terrestrial insects (Clissold and Simpson 2015, Corrêa *et al.* 2021, Kingsolver *et al.* 2006, Rohner *et al.* 2017, Lee and Roh 2010), fish (McLeod *et al.* 2013) and turtles (Marn *et al.* 2017). In these studies, warming generally resulted in a rapid life cycle by increasing growth rates and decreasing age and size at maturity as well as survival probabilities. However, these thermal effects were often modulated by food availability. In particular, temperature and food availability can covary and impact ectotherm life history traits. Koussoroplis and Wacker (2016) showed that the effect of food restriction on life history traits is more severe when temperature moves away from the optimal temperature. Nevertheless, these previous studies did not fully investigated how the effects of temperature and food restriction on multiple life history traits combine to influence fitness and population demographic parameters (e.g. generation time and population growth rate). This is an important limitation as we need to determine how the combination of effects on multiple traits influence fitness to understand the adaptive value of plastic and evolutionary responses to environmental factors; the latter being the focus of several studies and intense debates in the literature on TSR (see Kingsolver and Huey 2008, Fryxell *et al.* 2020, Walters and Hassall 2006, Zamudio *et al.* 1995). In addition, almost all the studies mentioned above were conducted on small invertebrate species (but see McLeod *et al.* 2013 and Marn *et al.* 2017). As a result, we have very limited information on how temperature and food availability jointly influence life history traits of vertebrate predators. This is of importance as body size changes in predatory species can alter population structure and influence trophic interaction strength and food webs stability (Emmerson and Raffaelli 2004, Sentis *et al.* 2017, Osmond *et al.* 2017, Uzsko *et al.* 2022).

In this study, we address this gap by experimentally investigating growth, reproduction and survival probability of a vertebrate predatory species, the medaka fish (*Oryzias latipes*, Temminck & schlegel), raised at two temperatures (20 and 30 °C) with and without food restriction. Our objectives were to investigate whether (1) TSR is maintained under food-restricted conditions, (2) food restriction modulates the effects of temperature on the growth, fecundity and survival of a vertebrate predatory species and (3) the effects of temperature and food on individual traits affect fitness and demographic parameters. To this end, we implemented our empirical measurements of life history traits into Integral Projection Models (IPMs) to understand and predict how their combined effects determine mean fitness and generation time across our different treatments of temperature and food restriction. We hypothesized that warming would increase growth and fecundity but lower survival, leading to rapid life cycle (short generation time). Moreover, we hypothesized that these thermal effect would be modulated by food restriction, the latter would increase survival and selects for late maturation at larger body size. We therefore expected that food restriction would increase the population generation time. Overall, our aim was to better understand to which extent investigating growth, reproduction and survival patterns could help disentangling the relative impacts of temperature and resource availability on body size shifts under global warming as well as understanding the adaptive values of these phenotypic responses.

Material and methods

Biological system and rearing conditions

The medaka is a small iteroparous freshwater fish native to East Asia (Hirshfield 1980). The life span of a medaka is about 2 years and its adult size varies between 30 and 50 mm (Ding *et al.* 2010, Egami and Etoh, 1969). This is an eurythermal species (5 °C - 35 °C) with an optimum temperature of 25 °C (Dhillon and Fox 2004). At this temperature, the medaka requires only 10 to 12 weeks to reach sexual maturity. Fish were maintained in the laboratory using an open water system with water supply controlled by drip emitters (1 L.h⁻¹). Input water quality was maintained with mechanical, biological

and UV filtration with a pH of 7.5 at 16 °GH. Each tank (25 x 40 x 20 cm) was equipped with an air filter to prevent high nitrite concentrations and maintain oxygen at saturation.

The parental F₀ generation consisted in a total of 76 fish (approximately 120 days old) of the CAB strain provided by Carolina Biological Supply Company (Burlington, NC, USA ; from AMAGEN, Gif-sur-Yvette, France) and WatchFrog (Evry, France). At reception, fish were kept for 5 days at 25 °C. Then, half of the fish were placed into five 20 L tanks for the "cold" thermal regime and the other half were placed into five 20 L tanks for the "warm" thermal regime. The female to male sex ratio per tank ranged from 1.33 to 1.66. The tank temperatures were increased or decreased by 0.5 °C every days until they reached 30 °C or 20 °C. During this acclimation period, the photoperiod was 12h: 12h (day: night) and, after acclimation, it was then adjusted to 16h: 8h (day: night) which is optimal for medaka reproduction (Hirshfield 1980).

From this F₀ generation, about 300 eggs were collected in each tank. Eggs were placed in small nurseries (2.5 L) made of fine mesh and each nursery was placed in the tank where the eggs were collected from (see Hemmer-Brepson *et al.* 2014, Loisel *et al.* 2019 for more details). After 30 days of growth, the parents were removed and the F₁ fish larvae were reared under four different treatment: ad_20 (*ad libitum* and 20 °C), res_20 (restriction and 20 °C), ad_30 (*ad libitum* and 30 °C) and res_30 (restriction and 30 °C). For each treatment, the growth of approximately 80 fish was monitored, except for res_20 where only 54 fish could be maintained. Fish were maintained in 20 L aquaria with 20 - 30 fish of a single treatment. This density (less than 2 - 3 fish per liter) does not cause any stress or agonistic behaviour in this species (Denny *et al.* 1991). The fish were fed with TetraMin® (composition: 47 % protein, 10 % fat content, 3 % cellulose and 6 % water) every morning (for the *ad libitum* condition) or every two mornings (for the restriction condition). On each feeding days, TetraMin® was provided to each tank until the fish no longer went up to the surface to get food. Excess food was systematically removed after feeding to prevent feeding between two meals. Apart from temperature and food, all the experimental parameters were similar in the four treatments.

The species-specific optimal thermal range for TSR is the range between the temperature at which the population growth rate becomes positive, and the temperature at which population growth rate is maximal (Walczyńska *et al.* 2016). Outside of this thermal range, the TSR pattern may not be observed, although the TSR can be maintained for temperatures slightly above the optimal temperature (Walczyńska *et al.* 2016). Yamamoto (1975) and Hirshfield (1980) reported that the optimal temperature for medaka reproduction is 27 °C, suggesting that the population growth rate is maximal at this temperature. Furthermore, Dhillon and Fox (2007) showed that individual growth rate did not differ for medakas reared at 27 °C or 30 °C, suggesting that our experimental temperatures are within the “optimal thermal range” for TSR and that our results are not the product of a response to a thermal stress.

Growth, fecundity and survival

The total length (from the head to the tip of the caudal fin, TL) of each fish was measured with a precision of 0.5 mm at 30, 45, 60, 100, 150, 200, 300 and 350 days. Fish were measured after placing them on a 5 cm diameter Petri dish layered with a millimeter graph paper and filled with water. They were then immediately released into their respective tank. An average of 150.6 ± 18.1 fish were measured per age (see Fig. S 1 for more details). As fish were not identified individually, the growth curves applies to the experimental population (i.e. one curve per treatment) and not to individuals. The investment in reproduction was quantified from sexual maturity by counting the number of eggs laid per female per day in each tank. The survival probability from 60 days (age of first sexually mature fish), referred to as survival in this study, was monitored daily until the end of the experiment.

Statistical analysis

TL measurements and ages were used to fit von Bertalanffy growth curve model (Von Bertalanffy 1938):

$$L_t = L_{\infty}(1 - e^{-K(t-t_0)}) \text{ (eq. 1)}$$

Where L_t is the estimated total length at time t , L_∞ the maximum asymptotic size (i.e. the total length for fish with an ∞ age), K the initial growth rate, and t_0 the theoretical age at which body size is null. Von Bertalanffy growth curves parameters (L_∞ , K , t_0) were estimated by Bayesian inference using the Bayesian software JAGS and the "R2jags" package (Su and Yajima, 2015) in R software (version 4.0.2; R development Core Team). We assumed that the asymptotic size L_∞ , the initial growth rate K , and the theoretical age at null size t_0 could vary between temperature (T) and resource (C) condition. Consequently, four values of L_∞ , K and t_0 (one for each combination (CT) of temperature and resource condition) were fitted. For each parameter, we used a normal uninformative prior with a mean of 0 and a precision parameter (inverse of the variance) of 0.001:

$$L_{\infty CT} \sim N(0, 0.001) \quad K_{CT} \sim N(0, 0.0001) \quad t_{0CT} \sim N(0, 0.001) \quad (\text{eq. 2})$$

To account for tanks (t) variability, we estimated random effects ε for each parameter using a multivariate normal distribution, $\varepsilon \sim N(0, \Sigma)$. The covariance matrix $\Sigma_{(3,3)}$ was defined as:

$$\begin{vmatrix} \sigma_{L_\infty}^2 & r_1 \cdot \sigma_{L_\infty} \cdot \sigma_K & r_2 \cdot \sigma_{L_\infty} \cdot \sigma_{t_0} \\ r_1 \cdot \sigma_{L_\infty} \cdot \sigma_K & \sigma_K^2 & r_3 \cdot \sigma_K \cdot \sigma_{t_0} \\ r_2 \cdot \sigma_{L_\infty} \cdot \sigma_{t_0} & r_3 \cdot \sigma_K \cdot \sigma_{t_0} & \sigma_{t_0}^2 \end{vmatrix} \quad (\text{eq. 3})$$

With σ_{L_∞} , σ_K , σ_{t_0} the standard deviations of each random vector, one per parameter, and r_1 , r_2 , r_3 the correlations between these vectors. We used uninformative priors with a uniform distribution for each parameter of Σ , adapting the limits to the parameters (e.g between -1 and 1 for a correlation).

$L_{\infty CT}$, K_{CT} and t_{0CT} are thus hyperpriors (population parameters) that serve to assess parameters for each tank (t) when associated with the random effects. For instance for the L_∞ parameter:

$$L_{\infty t} = L_{\infty CT} + \varepsilon_{L_{\infty t}} \quad (\text{eq. 4})$$

We then used (eq. 1) to estimate the expected mean total length L_{tj} for each tank (t), and each age (j):

$$L_{tj} = L_{\infty t} \left(1 - e^{-K_t(t_j - t_{0t})} \right) \quad (\text{eq. 5})$$

197 Finally, we hypothesized that the observed total length of each fish (f), L , was normally distributed:

$$198 \quad \begin{aligned} L_{ftj} &\sim N(L_{tj}, \sigma) \\ \sigma &\sim U(0,10) \end{aligned} \text{(eq. 6)}$$

199 To compare the growth patterns among temperature and resource conditions, we plotted the average
 200 growth curves for each treatment (combination of food condition and temperature), and their
 201 credibility interval (CI) using the posterior distributions of the parameters ($L_{\infty CT}$, K_{CT} , t_{0CT}) that were
 202 obtained from five independent Monte-Carlo Markov Chains (see Fig. S 2 for more details on the
 203 estimated parameter values). For each chain, after an initial burning of 50 000 values, 400 000
 204 iterations were computed and we conserved one value every 200 iterations to limit autocorrelation
 205 between estimations. The posterior distributions for each average total length at age (L) were thus
 206 constituted of 10,000 values. The quantiles 2.5 % and 97.5 % were used to estimate credibility intervals
 207 CIs. We compared the growth curves among our four experimental treatments by investigating the
 208 overlap among their CIs. Curves were considered as significantly different when their CIs do not overlap
 209 (Pritchard *et al.* 2017).

210 We investigated the effects of temperature, food restriction and their interaction (fixed
 211 effects) on mean daily clutch size per female (log transformed) and survival probabilities using a linear
 212 mixed effects model (*lmer* function in the “lme4” package (Bates *et al.* 2015)) and a mixed effects Cox
 213 proportional hazards model (*coxme* function in the “coxme” package (Therneau *et al.* 2022)), respec-
 214 tively, with tank as random factor. For both models, analyses of deviance using Wald tests were pro-
 215 vided to test the significance of fixed parameters. We tested the assumptions of the mixed effects Cox
 216 proportional hazards model using the *cox.zph* function (“survival” package (Therneau *et al.* 2022))
 217 which correlates the corresponding set of scaled Schoenfeld residuals with time to test for
 218 independence between residuals and time (see Fig. S 3 for more details).

219 Integral Projection Modelling

220 Integral Projection Models are discrete-time, structured population models that estimate the
 221 asymptotic behaviour of populations by combining life history traits that can be discrete or continuous
 222 (Levin *et al.* 2021). We used our empirical measurement of life history traits to quantify the fitness of
 223 populations simulated by IPMs for our four experimental treatments of temperature and food
 224 restriction. To build an IPM, the first step is to represent the life cycle of the focal species. At each time
 225 step, an individual medaka has a probability s to survive. If it survives, it grows according to a growth
 226 function g . This individual has a chance to reproduce according to the function f_p , and if it reproduces,
 227 it produces a number of eggs according to the fecundity function f_n . In the model, the vital rates (s ,
 228 g , f_p , f_n) are functions of the fish body size at time t . The eggs have hatching and survival
 229 probabilities according to the function f_g , and the resulting juvenile fish have a size distribution f_d .
 230 Egg hatching rate, survival of juvenile and their size distribution are independent from the size of their
 231 parents.

232 We used a similar IPM structure as in Bogdan *et al.* (2021):

$$233 \quad n(z', t + 1) = \int_L^U K(z', z) n(z, t) dz \text{ (eq. 7)}$$

234 Where $n(z', t+1)$ is the size of the population at time $t+1$, z' is the state variable describing the
 235 population (i.e. body size in our model). $n(z', t+1)$ is obtained by integrating the product of $K(z', z)$ and
 236 $n(z, t)$ over the domain $[L, U]$. In our model, the lower bound L is the minimum fish size and the upper
 237 bound U is the maximum size. $K(z', z)$ is a bivariate kernel function that describes the transitions to state
 238 z' given the initial state of an individual z at time t . $K(z', z)$ consists of two sub-kernels P and F . P
 239 describes the survival and growth of fish at time t ($P = s \cdot g$) and F describes the number and body size
 240 of juveniles at time $t+1$ according to reproduction probability, hatching rate, juvenile survival and body
 241 size distribution ($F = f_p \cdot f_n \cdot f_g \cdot f_d$).

242 This yields to:

243
$$n(z', t + 1) = \int_L^U [P(z', z) + F(z', z)]n(z, t)dz \text{ (eq. 8)}$$

244 The analytical solutions of IPMs are very resource expensive. An alternative method to solve eq. 8 is
 245 to use the integration rule of the midpoint of the meshes along the domain $[L, U]$ (Ellner *et al.* 2016).
 246 In our model, the domain extends from the predicted size in log of a fish after 30 days (L) to the
 247 maximum observed size in log (U). The number of meshes along this domain was set to 400.

248 To obtain the survival function s , we used Kaplan-Meier estimate to compute the survival
 249 probability for each sampled age. We then associated survival probabilities to fish body size using the
 250 estimated age-size relationship from the fitted Von Bertalanffy model. Survival probability (s) in
 251 function of body size was estimated using a logistic equation for each experimental treatment of
 252 temperature and food restriction.

253 To obtain the growth function g , we predicted the size at t (L_t) (from 0 to 350 days) of 10,000
 254 fish from the 10,000 combinations of Von Bertalanffy parameters from the Bayesian model posterior
 255 distributions. We then calculated the size at $t+1$ (L_{t+1}) from L_t following the formula:

256
$$L_{t+1} = L_t \cdot e^{-K} + L_{\infty} \cdot (1 - e^{-K}) \text{ (eq. 9)}$$

257 For each age, we computed the standard deviation of the sizes at $t+1$ (10,000 values), and then
 258 considered the average value of the standard deviations to implement residual variation around
 259 growth (g).

260 For the reproduction probability (f_p), we used a logistic equation considering that all fish reproduce
 261 once they reach their treatment-dependent age at maturity. For the fecundity function (f_n), we used
 262 a Poisson regression model to describe the link between fish size and egg number. Egg hatching rate
 263 and survival probability (f_g) and the body size distribution of juveniles (f_d) were estimated from
 264 unpublished data from the same experimental populations.

We used the "ipmr" R package functions to define the kernels (*define_kernel*), the domain (*define_domains*), and the initial state of the population (*define_pop_state*), and to compute the IPMs (*make_ipm*). The number of iterations of the IPMs was fixed per treatment to achieve asymptotic dynamics according to the *is_conv_to_asymptotic* function. We used the *gen_time* and *lambda* functions from the "Rage" and "ipmr" R packages to quantify the generation time T and the asymptotic *per capita* population growth rate λ . We quantified the uncertainty of T and λ by bootstrapping 1000 combinations of L_∞ , K and t_0 from the Bayesian model posterior distributions (with replacement) and by using 1000 random sample of each vital rate data set (survival, reproduction and fecundity) and refitting all demographic functions s, g, f_p, f_n . For each new iteration, we ran an IPM and estimated T and λ . This yielded 1000 estimates of T and λ for each experimental treatments. We next calculated the 95 % confidence intervals of T and λ and compared their mean values across experimental treatments based on the overlap of their 95 % confidence intervals. We also performed a sensitivity analysis to investigate the sensitivity of T and λ to small changes in the vital rate estimates (see Fig. S 5). Data and scripts used to build the IPMs and perform the sensitivity analysis are available online.

Results

We found that, under *ad libitum* conditions, warming leads to crossed growth curves by increasing initial growth rate and decreasing adult size (Figure 2). The same pattern was observed under food restriction, although the curves crossed later for the food-restricted fish compared to *ad libitum* fish. Food restriction in the cold treatment leads to nested growth curves throughout the experiment by decreasing the initial growth rate and adult size. Growth curves also tended to be nested in the warm treatment although the credibility intervals overlapped until day 149 and the curves were only significantly different toward the end of the experiment (from day 149 to day 316, Figure 2).

In the warm treatment, the fish were sexually mature at 67.3 ± 2.3 days (body length: 16.8 ± 0.1 mm) under *ad libitum* condition and at 60 days for all replicates (body length: 17.2 ± 0.7 mm) under

food restriction. In the cold treatment, they were sexually mature at 169.7 ± 0.6 days (body length: 26.3 ± 0.6 mm) and 186.5 ± 0.7 days (body length: 25.7 ± 0.4 mm) under *ad libitum* and food restriction conditions, respectively (Figure 3). We found that warming increased mean daily clutch size per female ($df = 1$, $Chi^2 = 13.26$, $p < 0.001$) and food restriction decreased it ($df = 1$, $Chi^2 = 10.58$, $p = 0.001$). Mean daily clutch size per female was not dependent on the interaction between temperature and food conditions ($df = 1$, $chi^2 = 0.79$, $p = 0.37$).

The fish survival was not significantly affected by the interaction between warming and food restriction ($Chi^2 = 0.70$, $df = 1$, $p = 0.40$, $n = 292$). In contrast, warming significantly reduced the fish survival ($Chi^2 = 6.96$, $df = 1$, $p = 0.01$, $n = 292$). Moreover, food restriction significantly increased survival ($Chi^2 = 15.04$, $df = 1$, $p < 0.001$, $n = 292$) (Figure 4).

We found that warming decreased generation time T and increased the asymptotic *per capita* population growth rate λ (Figure 5). In the cold treatment, food restriction significantly increased T and λ . Food restriction had no significant effect on T and λ in the warm treatment as their 95 % confidence intervals overlapped.

Discussion

Shrinking body size with increasing temperature has been proposed as a third universal response to global warming (Daufresne *et al.* 2009, Gardner *et al.* 2011). In addition, resources are expected to change with global warming (De Senerpont Domis *et al.* 2014), in response to changes in physicochemical, phenological (Visser and Both, 2005) and geographical parameters (Parmesan and Yohe, 2003). The independent and interactive effects of temperature and food availability on life history traits have been mainly studied in small aquatic (Betini *et al.* 2020, Giebelhausen and Lampert 2001, Wojewodzic *et al.* 2011, Persson *et al.* 2011, Giberson and Rosenberg 1992) and terrestrial (Clissold and Simpson 2015, Corrêa *et al.* 2021, Rohner *et al.* 2017, Lee and Roh 2010) invertebrate species. However, we have limited information on how temperature and food availability jointly influence life history traits in vertebrate predators and how the integration of these traits may

influence population fitness. Our objective was thus to test whether food availability can modulate the effects of temperature on size at age and life history traits of a vertebrate predator species, the medaka fish, and to investigate how these traits can affect population demographic parameters and life history strategies.

The results of our laboratory experiment indicate that, in agreement with the TSR rule (Atkinson and Sibly 1997, Berrigan and Charnov 1994, Arendt 2011), warming leads to crossed growth curves with individuals growing faster but reaching a smaller size at maturity and adult size compared to the cold condition. We conducted a short synthesis of the results of previous experimental studies investigating the responses in size at maturity or adult size to warming and food conditions (see Table S 1). This synthesis shows the important variability in the responses of size at maturity or adult size to temperature and food and the complexity of understanding the mechanisms underlying the control of body size in ectotherms. In line with our results, warming generally leads to a decrease in size at maturity and adult size in experimental studies (Table S 1). Nevertheless, some studies reported that temperature does not affect size at maturity or adult size, or can even increase body size (Table S 1). We found that food restriction does not affect size at maturity but leads to nested curves where restricted fish are smaller than non-restricted fish for each given age. These results are consistent with other experimental studies reporting that food restriction decreases adult size but does not affect size at maturity (Table S 1). In contrast, Giebelhausen and Lampert (2001), Courtney Jones *et al.* (2015), and Rohner *et al.* (2017) found a decrease in size at maturity under food restriction. Furthermore, the food restriction effects appeared to be greater at 20 °C where the growth curve for the restricted fish was more nested (i.e. below the curves for non-restricted fish) than at 30 °C. This is surprising because we expected food restriction to have more effect in warm treatment (as reported in McLeod *et al.* 2013, Wojewodzic *et al.* 2011, and Persson *et al.* 2011, Giberson and Rosenberg 1992) because warming increases metabolic rates which implies higher energy demand and feeding rate to sustain high metabolic costs (Brown *et al.* 2004). For instance, Betini *et al.* (2020) found a TSR amplification under food restriction with a body size reduction under warming five time stronger under food

restriction than under unlimited food conditions. Wojewodziec *et al.* (2011) and Persson *et al.* (2011) also reported that warming further amplifies the decrease in somatic growth rates of *Daphnia* under low nutritional quality (high C:P ratio) compared to *Daphnia* under high nutritional quality (low C:P ratio). These results suggest that temperature-induced body size shifts depend on the quantity but also the quality of resources with lower resource quality amplifying the detrimental effect of warming as reported in a recent study (Sentis *et al.* 2022). In addition to temperature and food, oxygen also appears to be a key factor controlling body size. In particular, TSR tends to be amplified under oxygen limitation (Frazier *et al.* 2001, Hoefnagel and Verberk 2015, Verberk *et al.* 2021). One of the most important differences between oxygen and food availability is that the former generally decreases with increasing temperature, while the latter may increase or decrease with warming. Walczyńska and Sobczyk (2017) suggested that TSR is a plastic response to temperature-dependent oxygen availability, but that food conditions should be controlled as a factor that shapes the strength of TSR.

For several species, warming leads to early maturation and increased fecundity (Betini *et al.* 2020, Marn *et al.* 2017, Giebelhausen and Lampert 2001). Our results are in line with these studies as we found that fish reared at 30 °C were sexually mature at a younger age and produced a larger mean daily clutch size per female. In contrast, less is known about the responses of developmental rates and fecundity to covariation between temperature and food. Our results did not suggest any effect of food restriction on age at maturity, in contrast to Betini *et al.* (2020) and Marn *et al.* (2017), who found that increased food availability resulted in earlier maturation. However, we found that food restriction decreased mean daily clutch size at both temperature conditions. Several studies have also found that increased food availability increased fecundity in both aquatic (Betini *et al.* 2020, Giberson and Rosenberg 1992) and terrestrial (Corrêa *et al.* 2021) organisms. This can be explained by an increase in the amount of energy to be allocated to reproduction under unlimited food conditions.

In addition, the survival probability in our experiment was influenced by both temperature and food restriction. Indeed, fish reared at 30 °C had a lower survival than fish reared at 20 °C while food

restriction increased the survival under both temperature conditions. This beneficial effect of food restriction on survival was also observed in frog larvae (Courtney Jones *et al.* 2015) and daphnia (Betini *et al.* 2020). Lower food availability implies a decrease in metabolism and thus a lower production of oxidizing agents which contributes to slow down senescence and increase survival, resulting in a “eat little die old” strategy (Sohal and Weindruch, 1996, Gredilla *et al.* 2001, Speakman 2005, Pifferi *et al.* 2018). Our results potentially illustrates different developmental strategies. For example, at 30 °C, fish may have maintained a high growth rate despite food restriction in order to maintain a rapid life cycle, at the expense of lower survival. This hypothesis is supported by the fact that mortality was higher and sexual maturity was reached at a younger age and smaller size at 30 °C compared to 20 °C. Ultimately, measuring the fitness of the fish under the different conditions would help understanding if these strategies are adaptive or results from physiological constraints than are difficulty overpassed by evolutionary adaptations.

Although food restriction decreased the mean daily clutch size, these effects were relatively weak compared to the increase in survival. This may be explained by potential acclimation of medaka to rearing temperatures or by food restriction being not severe enough. Reducing feeding events by half (1 out of 2 mornings) was considered restrictive although we cannot exclude compensatory mechanisms were restricted fish would feed more when they have access to food. Although this remains to be investigated in more details, our results highlight the importance of considering the interactions between temperature, body size and food to understand how larger predatory species respond to global changes in terms of developmental and life history strategies. When we integrated our experimentally measured traits into integral projection models (IPM), we found a reduction in generation time and an increase in the population growth rate under warming. Although survival probability was lower under warming, fish reached sexual maturity much faster and had higher fecundity. The earlier sexual maturity of fish enabled them to reproduce for a longer time. Therefore, each female could produce a higher number of juveniles, which leads to a higher population growth rate compared to cold-acclimated populations. Consistent with our experimental data, the IPMs

revealed that food restriction had a greater impact on the generation time and growth rate of cold-acclimated populations compared to warm-acclimated populations. Specifically, food restriction increased generation time and asymptotic *per capita* population growth rate at 20 °C, whereas it had no significant effect on demographic parameters of the populations at 30 °C. Our experimental results showed that food restriction slightly decreased fecundity but strongly increased fish survival probability, resulting in longer individual lifespans and the production of more juveniles. Ultimately, food restriction proved evolutionarily advantageous in the cold treatment, leading to a population growth rate equals to unity ($\lambda = 1$). This indicates that the population moves from a declining dynamic ($\lambda < 1$) when food is not limiting to an increasing dynamic ($\lambda > 1$) under food restriction. Our sensitivity analyses revealed that the demographic parameters were mainly sensitive to the reproduction and survival probabilities (see Fig. S 5). These parameters determine the lifespan of the fish and the duration of their reproduction. The high sensitivity of the model to the reproduction probability can be explained by our assumption that, in the model, all females reproduce once they reach maturity (because lacked information on which female reproduces when) which lead to a steep reproduction function. Nevertheless, this assumption was similar for the four treatment and should not influence the qualitative comparison of our four treatments. Overall, IPMs allowed for the combination of traits and confirmed that population mean fitness increases with temperature, and that food restriction increases mean fitness at low temperature.

The ecological consequences of temperature-induced changes in body size are multiple. For instance, it can alter predator-prey size ratio which has important implications for the occurrence and strength of predator-prey interactions and thus for community dynamics and food web structure (Sentis *et al.* 2017, Yodzis and Innes 1992, Kalinkat *et al.* 2013, Vagnon *et al.* 2021, Emmerson and Raffaelli 2004, Williams and Martinez 2000). Size interacts with temperature because temperature alters the energetic demands of organisms. For example, higher temperatures can increase short-term predator-prey interaction strength and predator energetic efficiency (Sentis *et al.* 2012). To date, studies examining the consequences of temperature-induced body size shifts on trophic interactions,

community dynamics, and food web structure, only considered the reduction in adult size (Sentis *et al.* 2017, Osmond *et al.* 2017, Bideault *et al.* 2019). However, our results emphasize the importance of considering ontogeny in future studies as the temperature effect on growth are dependent on life stages. In addition, we expect phenological and geographic changes to alter the quantity and quality of resources (Winder and Schindler 2004, Paerl and Huisman 2008, Paerl 2014, Ekvall *et al.* 2013, Urrutia-Cordero *et al.* 2017), for example in predator-prey relationships by inducing temporal or spatial mismatches where the predator is left with reduced food availability (Boukal *et al.* 2019, Twining *et al.* 2022). Along the same line, Visser *et al.* (2006) showed that asynchrony between caterpillar biomass and the offspring feeding requirements of an insectivorous bird affected the number and weight of fledged birds. These phenological asynchronies can alter the structure and dynamics of food webs and modify ecosystem processes (Damien and Tougeron 2019, Renner and Zohner 2018). Altogether, these studies indicate that it is important to investigate the direct effects of temperature as well as indirect effects such as altered food quality and availability to better understand the impact of climate change on growth, survival and fecundity.

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722

723 Figures legend

724 **Figure 1:** Patterns of crossed vs. nested growth curves driven by (a) temperature and (b) food
725 availability (after Berrigan and Charnov 1994).

726 **Figure 2:** Fitted von Bertalanffy growth curve for each combination of temperature and food
727 conditions. Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C),
728 respectively. Solid and dotted lines represent the *ad libitum* and the food restriction treatments,
729 respectively. Areas represent the 95 % credibility intervals. Vertical bars represent age at maturity. As
730 fish were not identified individually, jittered points represent experimentally measured sizes (in mm)
731 at age (in days) of fish from different replicates (i.e.tanks).

732 **Figure 3:** Temperature and food restriction effects on mean daily clutch size per female.
733 Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively.
734 Filled and empty points and boxplot represent the *ad libitum* and food restriction treatments,
735 respectively.

736 **Figure 4:** Kaplan-Meier survival curves from 60 days for each combination of temperature and food
737 conditions. Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C),
738 respectively. Solid and dashed lines represent the *ad libitum* and the food restriction treatments,
739 respectively. Shaded areas around the lines represent the 95 % confident intervals.

740 **Figure 5:** Estimated (a) generation time T and (b) asymptotic per capita population growth rate λ for
741 each combination of temperature and food conditions. Black and red colors correspond to the cold
742 and warm treatments, respectively. Filled and empty circles correspond to the median of *ad libitum*
743 and food restriction treatments, respectively. Bars represent 95 % confident intervals.

744 Appendix

745 **Fig. S 1:** Number of fish measured at different ages.

746 **Fig. S 2 :** Estimated Von Bertalanffy parameters for each treatment. Black and red colors correspond
747 to the cold and warm treatments, respectively. Filled and empty circles correspond to the median of
748 *ad libitum* and food restriction treatments, respectively. Bars represent 95 % credibility intervals.

749 Consistent with the experimental curves and TSR, warming significantly increased the initial
750 growth rate K and decreased the maximum asymptotic size L_{∞} . Food restriction had no effect on the
751 initial growth rate K for fish reared at 30 °C, but significantly reduced K for fish reared at 20 °C. At the
752 end of our experiment, the adult size of food restricted fish was smaller than that of *ad libitum* fed
753 fish, especially at 20 °C. Yet, food restriction had no significant effect on the maximum asymptotic size
754 L_{∞} , indicating that beyond 350 days, fish should reach the same size regardless of their food condition.
755 Extrapolating to 700 days (life span of a medaka) from our experimental curves, restricted fish should
756 reach the same adult size as *ad libitum* fed fish at approximately 400 and 300 days under cold and
757 warm conditions, respectively (Fig. S 4). The theoretical age at which body size is zero t_0 was not
758 significantly different between temperature conditions.

759 **Fig. S 3:** Cox model assumption of proportionality for temperature and food condition.

760 The *cox.zph* function correlates the scaled Schoenfeld residuals with time for each covariate to
761 test for independence between residuals and time. Additionally, it performs a global test for the model
762 as a whole. From our model output, this test was not statistically significant for temperature ($\chi^2 =$
763 0.20 , $df = 1$, $p = 0.65$), food ($\chi^2 = 0.00$, $df = 1$, $p = 0.97$) and the global test ($\chi^2 = 0.20$, $df = 2$, $p = 0.90$),
764 indicating a proportional hazards.

765 **Fig. S 4:** Extrapolation of Von Bertalanffy growth curve for each combination of temperature and food
766 conditions. Black and red colors represent the cold and warm treatments, respectively. Solid and

dotted lines represent the *ad libitum* and the food restriction treatments, respectively. Areas represent the 95 % credibility intervals. Points represent experimentally measured sizes at age.

Table S 1: Responses in size at maturity and adult size to warming and food increase in the experimental studies. The symbols +, - and x indicate a positive, negative or no effect of the variable, respectively.

Persson *et al.* (2011) and Wojewodzic *et al.* (2011) were not included in this table as they looked at the individual somatic growth rate SGR (which differs from the size at maturity or adult size). They found that SGR of daphnia increased with temperature, but that this effect depended on the C:P ratio of the food. The higher the temperature, the more phosphorus limitation decreased the SGR.

Fig. S 5: Sensitivity analysis of (a) asymptotic per capita population growth rate λ and (b) generation time T . Black and red colors correspond to the cold and warm treatments, respectively. Filled and empty circles correspond to the median of *ad libitum* and food restriction treatments, respectively.

We performed sensitivity analyses to investigate the sensitivity of generation time T and the asymptotic per capita population growth rate λ to small changes in the values of vital rates. To do so, we added or subtracted 1 % to the slope of the relationships between survival, reproductive probability or fecundity and body size. For the parameters that are independent of body size, we added or subtracted 1 % to the mean value. For the growth function, we also modified K and L_{∞} by adding or subtracting 1 % to their mean values. We then investigated the sensitivity of T and λ by calculating the log ratio of the parameter (λ or T) estimated by the model with a change of 1 % in a single variable to the parameter estimated by the baseline IPM model. The further the log of this ratio is away from 0, the more sensitive the demographic parameter is to the vital rate.

Demographic parameters are most sensitive to variability in reproductive probability. Since we consider all fish to reproduce with probability = 1 from sexual maturity, adding or subtracting 1 % to the slope of the regression is equivalent to increasing or decreasing age at sexual maturity by 13.7,

791 10.3, 2.4, and 1.8 days for conditions ad_20, res_20, ad_30, and res_30, respectively. Not surprisingly,
792 this input strongly influences the demographic parameters since in the model the length of time a fish
793 is fertile depends directly on age at maturity. Demographic parameters are also sensitive to the
794 probability of survival. As with the probability of reproduction, this survival probability also determines
795 the length of time a fish can produce eggs before it dies. Finally, the generation time is somewhat
796 sensitive to the K and L_{∞} parameters of the Von Bertalanffy model. By influencing growth, these
797 parameters will determine the rate at which a fish reaches size at sexual maturity in the model, and
798 thus the rate at which a fish can reproduce, directly impacting generation time.