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

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Abstract

The reduction of body size with warming has been proposed as the third universal response to global warming, besides geographical and phenological shifts. 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. Nevertheless, climate warming can decrease food availability by modifying biochemical cycles and primary production. Food availability can also influence growth, fecundity and survival and thus potentially modulate the effect of temperature on life history strategies and fitness. However, the interactive effects of temperature and food availability on life history traits have been mostly studied in small invertebrate species where life history traits have been mainly considered in isolation. In contrast, we have limited information on (1) how temperature and food availability jointly influence life history traits in vertebrate predators and (2) how changes in different life history traits combines to influence fitness and population growth. To fill this gap, we investigated under laboratory conditions the independent and interactive effects of temperature (20 or 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 generation time and population growth rate (i.e. mean fitness). Our results confirm that 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 corresponding to a "eat little die old" strategy. 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 highlight the importance of accounting for the interaction between temperature and food availability to understand how body size shifts can

affects vital rates and population demography. This is of importance in the context of global warming as resources (e.g., phytoplankton and zooplankton communities in aquatic ecosystems) are predicted to change in size structure and total abundance with increasing temperatures. Interestingly, our results suggest that food restriction has a weaker effect on fish mean fitness under warming.

Key-words: climate change, food restriction, temperature, TSR, strategy, life-history traits, fish, Integral Projection Model.

Introduction

Body size reduction has been proposed as a third universal species response to global warming (Daufresne *et al.* 2009, Gardner *et al.* 2011, Sheridan and Bickford 2011), in addition to changes in phenology (Visser and Both 2005) and geographic distribution (Parmesan and Yohe 2003). While the first two responses have been studied extensively (Meyer *et al.* 1999), the third one has received less attention despite its high prevalence and magnitude. For instance, body size can reduce up to -4 % per °C in terrestrial species and up to -8 % per °C in aquatic ectotherms (Forster *et al.* 2012). Previous studies focused on proximal mechanisms, (i.e. how environmental factors influence life history traits by impacting physiological and developmental processes (Thierry 2005)) and ultimate mechanisms related to the evolution and adaptive value of body size changes (Zuo *et al.* 2012, Atkinson and Sibly 1997, Frazier *et al.* 2001, Hoefnagel and Verberk 2015, Walczyńska *et al.* 2015, Verberk *et al.* 2021) and their variability among species and habitats (Horne *et al.* 2015, Forster *et al.* 2012, Atkinson 1994). In aquatic systems, warming decreases oxygen concentration and hypoxia tends to amplify TS responses, which has been interpreted as a response to limited oxygen resource (Frazier *et al.* 2001, Hoefnagel and Verberk 2015, Verberk *et al.* 2021). In contrast, in terrestrial system, oxygen is less limiting and other factors may be more important than oxygen concentration. For instance, the risks of not completing juvenile development in time before the onset of winter strongly determine growth pattern in terrestrial organisms whereas it has less influence in the growth of aquatic organisms (Verberk *et al.* 2021). These differences may explain why TS responses are weaker in terrestrial than in aquatic ecosystems (Forster *et al.* 2012). At the individual level, body size shift can be explained by the "Temperature Size Rule" (TSR, Atkinson 1994, Atkinson and Sibly 1997, Angilletta *et al.* 2004, Berrigan and Charnov 1994, Perrin 1995, Arendt 2007, Arendt 2011), which states that ectotherms grow faster but reach a smaller size at a given stage of development (e.g. size at maturity or adult size) under warm environment compared to colder ones, resulting in "crossed" growth curves (Figure 1). This pattern of TSR remains an evolutionary puzzle (Atkinson and Sibly 1997) and body size shifts could be 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 (Marn *et al.* 2017, Courtney Jones *et al.* 2015, Corrêa *et al.* 2021, Clissold and Simpson 2015, Kingsolver *et al.* 2006, 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 Marn *et al.* 2017, Corrêa *et al.* 2021, Kingsolver *et al.* 2006) 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.

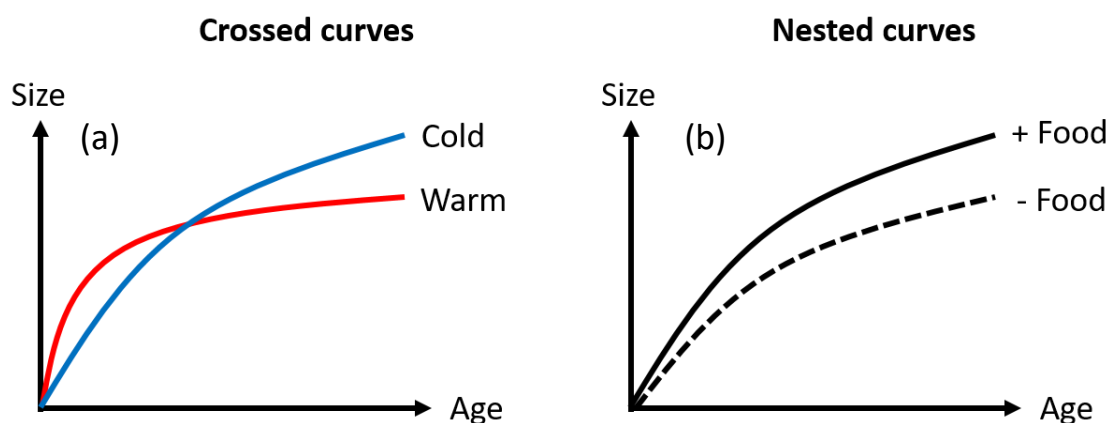


Figure 1: Patterns of crossed vs. nested growth curves driven by (a) temperature and (b) food availability (after Berrigan and Charnov 1994).

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 F_0 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 F_0 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 F_1 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:

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

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:

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

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:

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

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

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

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

$$L_{ftj} \sim N(L_{tj}, \sigma) \text{ (eq. 6)}$$

$$\sigma \sim U(0, 10)$$

To compare the growth patterns among temperature and resource conditions, we plotted the average growth curves for each treatment (combination of food condition and temperature), and their

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

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

Integral Projection Modelling

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

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

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

Where $n(z', t+1)$ is the size of the population at time $t+1$, z' is the state variable describing the population (i.e. body size in our model). $n(z', t+1)$ is obtained by integrating the product of $K(z', z)$ and $n(z, t)$ over the domain $[L, U]$. In our model, the lower bound L is the minimum fish size and the upper bound U is the maximum size. $K(z', z)$ is a bivariate kernel function that describes the transitions to state z' given the initial state of an individual z at time t . $K(z', z)$ consists of two sub-kernels P and F . P describes the survival and growth of fish at time t ($P = s \cdot g$) and F describes the number and body size

274 of juveniles at time $t+1$ according to reproduction probability, hatching rate, juvenile survival and body
 275 size distribution ($F = f_p \cdot f_n \cdot f_g \cdot f_d$).

276 This yields to:

$$277 \quad n(z', t + 1) = \int_L^U [P(z', z) + F(z', z)]n(z, t)dz \text{ (eq. 8)}$$

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

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

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

$$290 \quad L_{t+1} = L_t \cdot e^{-K} + L_\infty \cdot (1 - e^{-K}) \text{ (eq. 9)}$$

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

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

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

313

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).

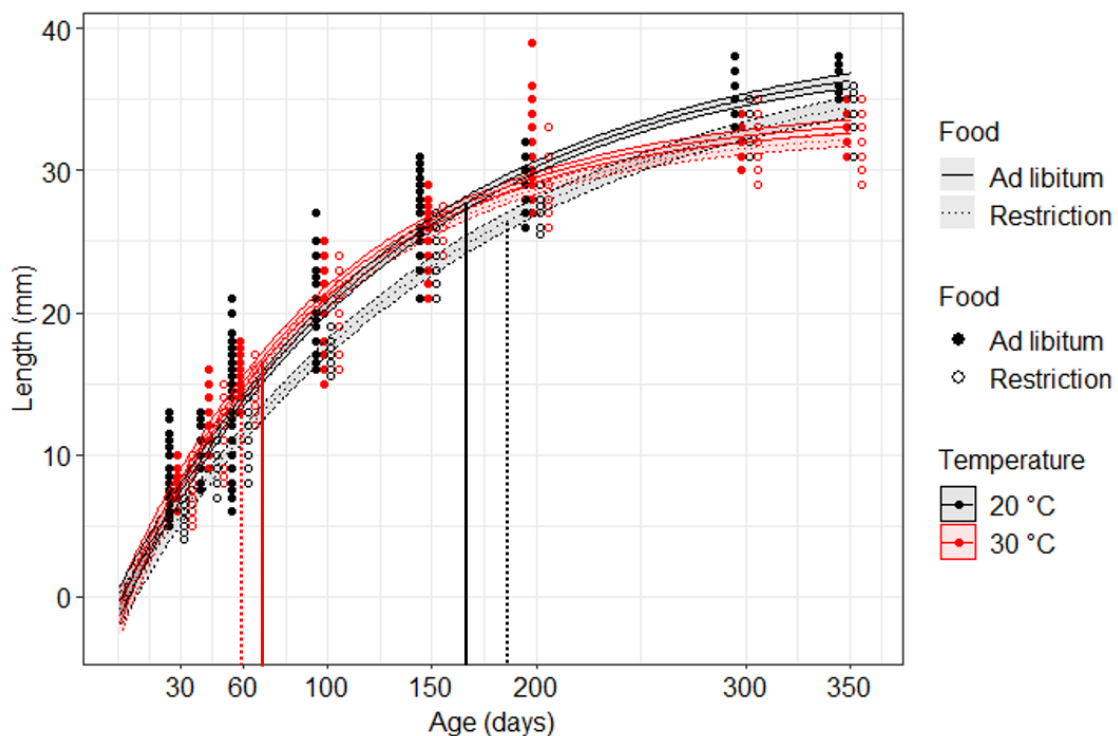


Figure 2: Fitted von Bertalanffy growth curve for each combination of temperature and food conditions. Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively. Solid and dotted lines represent the *ad libitum* and the food restriction treatments, respectively. Areas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

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 ($df = 1$, $chi^2 = 0.79$, $p = 0.37$).

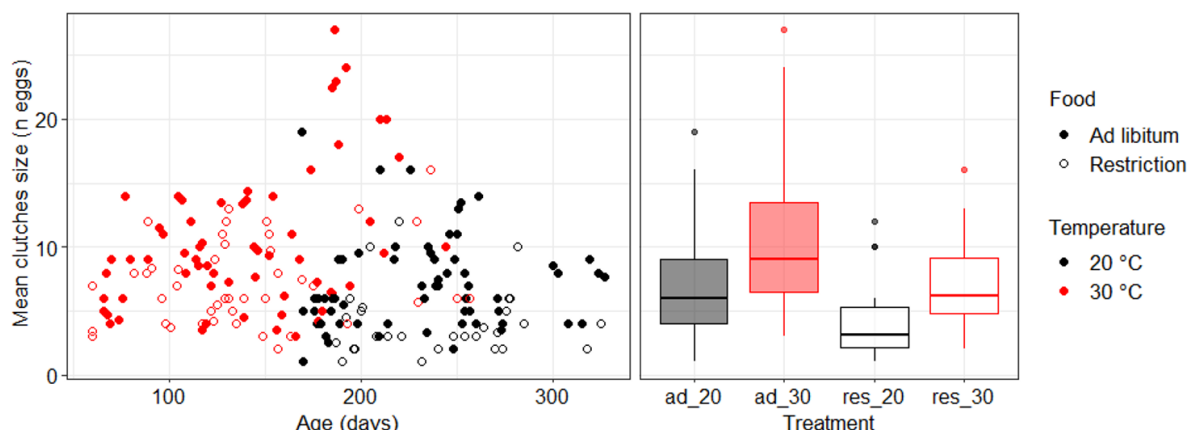


Figure 3: Temperature and food restriction effects on mean daily clutch size per female.
 Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively.
 Filled and empty points and boxplot represent the ad libitum and food restriction treatments, respectively.

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).

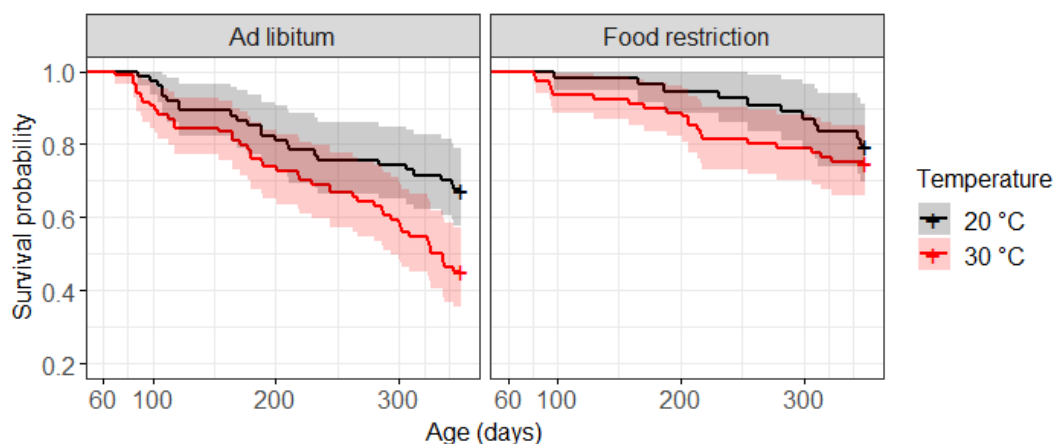


Figure 4: Kaplan-Meier survival curves from 60 days for each combination of temperature and food conditions.
 Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively. Solid and dashed lines represent the ad libitum and the food restriction treatments, respectively.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

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.

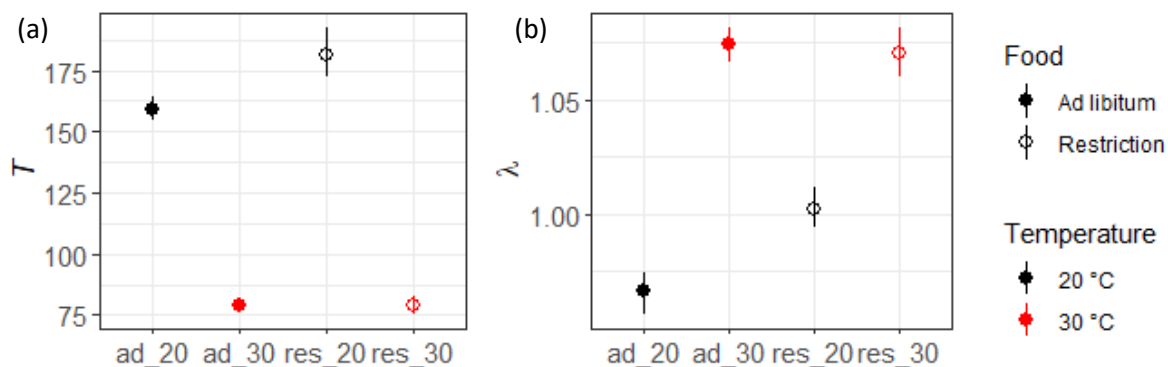


Figure 5: Estimated (a) generation time T and (b) asymptotic per capita population growth rate λ for each combination of temperature and food conditions.

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. Bars represent 95 % confident intervals.

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. Wojewodzic *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 Weindrich, 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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Data, scripts and codes availability

Data, scripts and code are available online : <https://doi.org/10.6084/m9.figshare.20375850.v12>

Conflict of interest disclosure

The authors of this preprint declare that they have no financial conflict of interest with the content of this article.

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References

- Angilletta, Michael J., Jr., Todd D. Steury, and Michael W. Sears. 2004. "Temperature, Growth Rate, and Body Size in Ectotherms: Fitting Pieces of a Life-History Puzzle1". *Integrative and Comparative Biology* 44 (6): 498-509. <https://doi.org/10.1093/icb/44.6.498>.
- Arendt, Jeff. 2007. "Ecological Correlates of Body Size in Relation to Cell Size and Cell Number: Patterns in Flies, Fish, Fruits and Foliage." *Biological Reviews* 82 (2): 241–56. <https://doi.org/10.1111/j.1469-185X.2007.00013.x>.
- Arendt, Jeffrey D. 2011. "Size-Fecundity Relationships, Growth Trajectories, and the Temperature-Size Rule for Ectotherms." *Evolution* 65 (1): 43–51. <https://doi.org/10.1111/j.1558-5646.2010.01112.x>.
- Atkinson, D. 1994. "Temperature and Organism Size—A Biological Law for Ectotherms?" In *Advances in Ecological Research*, edited by M. Begon and A. H. Fitter, 25:1–58. Academic Press. [https://doi.org/10.1016/S0065-2504\(08\)60212-3](https://doi.org/10.1016/S0065-2504(08)60212-3).
- Atkinson, David, and Richard M. Sibly. 1997. "Why Are Organisms Usually Bigger in Colder Environments? Making Sense of a Life History Puzzle." *Trends in Ecology & Evolution* 12 (6): 235–39. [https://doi.org/10.1016/S0169-5347\(97\)01058-6](https://doi.org/10.1016/S0169-5347(97)01058-6).

- 524 Bates, Douglas, Martin Mächler, Ben Bolker, and Steve Walker. 2015. "Fitting Linear Mixed-Effects
525 Models Using lme4." *Journal of Statistical Software* 67 (October): 1–48.
526 <https://doi.org/10.18637/jss.v067.i01>.
- 527 Berrigan, D., and E. L. Charnov. 1994. "Reaction Norms for Age and Size at Maturity in Response to
528 Temperature: A Puzzle for Life Historians." *Oikos* 70 (3): 474–78. <https://doi.org/10.2307/3545787>.
- 529 Bertalanffy, Ludwig Von. 1938. "A quantitative theory of organic growth (inquiries on growth laws.
530 li)." *Human Biology* 10 (2): 181–213. <https://www.jstor.org/stable/41447359>.
- 531 Bestion, Elvire, Aimeric Teyssier, Murielle Richard, Jean Clobert, and Julien Cote. 2015. "Live Fast, Die
532 Young: Experimental Evidence of Population Extinction Risk Due to Climate Change." *PLOS Biology* 13
533 (10): e1002281. <https://doi.org/10.1371/journal.pbio.1002281>.
- 534 Betini, Gustavo S., Xueqi Wang, Tal Avgar, Matthew M. Guzzo, and John M. Fryxell. 2020. "Food Avail-
535 ability Modulates Temperature-Dependent Effects on Growth, Reproduction, and Survival in *Daphnia*
536 *Magna*." *Ecology and Evolution* 10 (2): 756–62. <https://doi.org/10.1002/ece3.5925>.
- 537 Bideault, Azenor, Michel Loreau, and Dominique Gravel. 2019. "Temperature Modifies Consumer-
538 Resource Interaction Strength Through Its Effects on Biological Rates and Body Mass". *Frontiers in*
539 *Ecology and Evolution* 7. <https://www.frontiersin.org/article/10.3389/fevo.2019.00045>.
- 540 Boersma, Maarten, and Jacobus Vijverberg. 1996. "Food Effects on Life History Traits and Seasonal
541 Dynamics of *Ceriodaphnia Pulchella*." *Freshwater Biology* 35 (1): 25–34.
542 <https://doi.org/10.1046/j.1365-2427.1996.00478.x>.
- 543 Bogdan, Ana, Sam C. Levin, Roberto Salguero-Gómez, and Tiffany M. Knight. 2021. "Demographic
544 Analysis of an Israeli *Carpobrotus* Population." *PLoS ONE* 16 (4): e0250879.
545 <https://doi.org/10.1371/journal.pone.0250879>.
- 546 Boggs, Carol L., and Charles L. Ross. 1993. "The Effect of Adult Food Limitation on Life History Traits
547 in *Speyeria Mormonia* (Lepidoptera: Nymphalidae)." *Ecology* 74 (2): 433–41.
548 <https://doi.org/10.2307/1939305>.
- 549 Boukal, David S, Azenor Bideault, Bruno M Carreira, and Arnaud Sentis. 2019. "Species Interactions
550 under Climate Change: Connecting Kinetic Effects of Temperature on Individuals to Community Dy-
551 namics." *Current Opinion in Insect Science, Global change biology • Molecular Physiology*, 35 (Octo-
552 ber): 88–95. <https://doi.org/10.1016/j.cois.2019.06.014>.
- 553 Brown, James H., James F. Gillooly, Andrew P. Allen, Van M. Savage, and Geoffrey B. West. 2004. "To-
554 ward a Metabolic Theory of Ecology." *Ecology* 85 (7): 1771–89. <https://doi.org/10.1890/03-9000>.
- 555 Calder, William A. 1996. *Size, Function, and Life History*. Courier Corporation.
- 556 Clissold, Fiona J, and Stephen J Simpson. 2015. "Temperature, Food Quality and Life History Traits of
557 Herbivorous Insects." *Current Opinion in Insect Science, Global change biology • Molecular physi-
558 ology*, 11 (October): 63–70. <https://doi.org/10.1016/j.cois.2015.10.011>.
- 559 Corrêa, Cindi P., Sheila S. Parreiras, Luiz A. Beijo, Paulo M. de Ávila, Isabel R. V. Teixeira, and Angel
560 Roberto Barchuk. 2021. "Life History Trait Response to Ambient Temperature and Food Availability
561 Variations in the Bean Weevil *Zabrotes Subfasciatus*." *Physiological Entomology* 46 (3–4): 189–99.
562 <https://doi.org/10.1111/phen.12358>.

- 563 Courtney Jones, Stephanie K., Adam J. Munn, Trent D. Penman, and Phillip G. Byrne. 2015. "Long-
564 Term Changes in Food Availability Mediate the Effects of Temperature on Growth, Development and
565 Survival in Striped Marsh Frog Larvae: Implications for Captive Breeding Programmes." *Conservation*
566 *Physiology* 3 (1): cov029. <https://doi.org/10.1093/conphys/cov029>.
- 567 Cross, Wyatt F., James M. Hood, Jonathan P. Benstead, Alexander D. Huryn, and Daniel Nelson. 2015.
568 "Interactions between Temperature and Nutrients across Levels of Ecological Organization." *Global*
569 *Change Biology* 21 (3): 1025–40. <https://doi.org/10.1111/gcb.12809>.
- 570 Damien, Maxime, and Kévin Tougeron. 2019. "Prey–Predator Phenological Mismatch under Climate
571 Change." *Current Opinion in Insect Science*, Global change biology • Molecular Physiology, 35 (Octo-
572 ber): 60–68. <https://doi.org/10.1016/j.cois.2019.07.002>.
- 573 Daufresne, Martin, Kathrin Lengfellner, and Ulrich Sommer. 2009. "Global Warming Benefits the
574 Small in Aquatic Ecosystems." *Proceedings of the National Academy of Sciences* 106 (31): 12788–93.
575 <https://doi.org/10.1073/pnas.0902080106>.
- 576 De Senerpont Domis, Lisette N., Dedmer B. Van de Waal, Nico R. Helmsing, Ellen Van Donk, and Wolf.
577 M. Mooij. 2014. "Community Stoichiometry in a Changing World: Combined Effects of Warming and
578 Eutrophication on Phytoplankton Dynamics." *Ecology* 95 (6): 1485–95. <https://doi.org/10.1890/13-1251.1>.
- 580 Denny, J., R. Spehar, K. Mead, and S. Yousuff. 1991. "Guidelines for Culturing the Japanese Medaka,
581 'Oryzias Latipes'." PB92137496. Environmental Research Lab.-Duluth, MN.; AScl Corp., Duluth, MN.
- 582 Dhillon, R. S., and M. G. Fox. 2007. "Growth-Independent Effects of a Fluctuating Thermal Regime on
583 the Life-History Traits of the Japanese Medaka (*Oryzias Latipes*)". *Ecology of Freshwater Fish* 16 (3):
584 425–31. <https://doi.org/10.1111/j.1600-0633.2007.00240.x>.
- 585 Dhillon, Rashpal S., and Michael G. Fox. 2004. "Growth-Independent Effects of Temperature on Age
586 and Size at Maturity in Japanese Medaka (*Oryzias Latipes*).". Edited by S. J. Beaupre. *Copeia* 2004 (1):
587 37–45. <https://doi.org/10.1643/CI-02-098R1>.
- 588 Ding, Lingling, Wendy W. Kuhne, David E. Hinton, Jian Song, and William S. Dynan. 2010. "Quantifia-
589 ble Biomarkers of Normal Aging in the Japanese Medaka Fish (*Oryzias Latipes*).". *PLoS ONE* 5 (10):
590 e13287. <https://doi.org/10.1371/journal.pone.0013287>.
- 591 Egami, N., and H. Etoh. 1969. "Life Span Data for the Small Fish, *Oryzias Latipes*." *Experimental Ger-*
592 *ontology* 4 (2): 127–29. [https://doi.org/10.1016/0531-5565\(69\)90035-7](https://doi.org/10.1016/0531-5565(69)90035-7).
- 593 Ekvall, Mattias K., Javier de la Calle Martin, Elisabeth J. Faassen, Susanne Gustafsson, Miquel Lürling,
594 and Lars-Anders Hansson. 2013. "Synergistic and Species-Specific Effects of Climate Change and Wa-
595 ter Colour on Cyanobacterial Toxicity and Bloom Formation." *Freshwater Biology* 58 (11): 2414–22.
596 <https://doi.org/10.1111/fwb.12220>.
- 597 Ellner, Stephen P., Dylan Z. Childs, and Mark Rees. 2016. "Data-Driven Modelling of Structured Popu-
598 lations: A Practical Guide to the Integral Projection Model". 1st ed. 2016 edition. New York, NY:
599 Springer.
- 600 Emmerson, Mark C., and Dave Raffaelli. 2004. "Predator–Prey Body Size, Interaction Strength and the
601 Stability of a Real Food Web." *Journal of Animal Ecology* 73 (3): 399–409.
602 <https://doi.org/10.1111/j.0021-8790.2004.00818.x>.

- Forster, Jack, Andrew G. Hirst, and David Atkinson. 2012. "Warming-Induced Reductions in Body Size Are Greater in Aquatic than Terrestrial Species." *Proceedings of the National Academy of Sciences* 109 (47): 19310–14. <https://doi.org/10.1073/pnas.1210460109>.
- Frazier, Melanie R., H. Arthur Woods, and Jon F. Harrison. 2001. "Interactive Effects of Rearing Temperature and Oxygen on the Development of *Drosophila Melanogaster*." *Physiological and Biochemical Zoology* 74 (5): 641–50. <https://doi.org/10.1086/322172>.
- Fryxell, David C., Alexander N. Hoover, Daniel A. Alvarez, Finn J. Arnesen, Javiera N. Benavente, Emma R. Moffett, Michael T. Kinnison, Kevin S. Simon, and Eric P. Palkovacs. 2020. "Recent Warming Reduces the Reproductive Advantage of Large Size and Contributes to Evolutionary Downsizing in Nature." *Proceedings. Biological Sciences* 287 (1928): 20200608. <https://doi.org/10.1098/rspb.2020.0608>.
- Gardner, Janet L., Anne Peters, Michael R. Kearney, Leo Joseph, and Robert Heinsohn. 2011. "Declining Body Size: A Third Universal Response to Warming?" *Trends in Ecology & Evolution* 26 (6): 285–91. <https://doi.org/10.1016/j.tree.2011.03.005>.
- Giberson, Donna J., and David M. Rosenberg. 1992. "Effects of Temperature, Food Quantity, and Nymphal Rearing Density on Life-History Traits of a Northern Population of *Hexagenia* (Ephemeroptera:Ephemeridae)." *Journal of the North American Benthological Society* 11 (2): 181–93. <https://doi.org/10.2307/1467384>.
- Gibert, Jean P., and John P. DeLong. 2014. "Temperature Alters Food Web Body-Size Structure." *Biology Letters* 10 (8): 20140473. <https://doi.org/10.1098/rsbl.2014.0473>.
- Giebelhausen, B., and W. Lampert. 2001. "Temperature Reaction Norms of *Daphnia Magna*: The Effect of Food Concentration." *Freshwater Biology* 46 (3): 281–89. <https://doi.org/10.1046/j.1365-2427.2001.00630.x>.
- Gredilla, Ricardo, Alberto Sanz, Monica Lopez-Torres, and Gustavo Barja. 2001. "Caloric Restriction Decreases Mitochondrial Free Radical Generation at Complex I and Lowers Oxidative Damage to Mitochondrial DNA in the Rat Heart." *The FASEB Journal* 15 (9): 1589–91. <https://doi.org/10.1096/fj.00-0764fje>.
- Hemmer-Brepson, C., L. Replumaz, C. Romestaing, Y. Voituron, and M. Daufresne. 2014. "Non-Stressful Temperature Effect on Oxidative Balance and Life History Traits in Adult Fish (*Oryzias Latipes*)." *The Journal of Experimental Biology* 217 (Pt 2): 274–82. <https://doi.org/10.1242/jeb.096172>.
- Hirshfield, Michael F. 1980. "An Experimental Analysis of Reproductive Effort and Cost in the Japanese Medaka, *Oryzias Latipes*." *Ecology* 61 (2): 282–92. <https://doi.org/10.2307/1935187>.
- Hoefnagel, K. Natan, and Wilco C. E. P. Verberk. 2015. "Is the Temperature-Size Rule Mediated by Oxygen in Aquatic Ectotherms?" *Journal of Thermal Biology, What sets the limit? How thermal limits, performance and preference in ectotherms are influenced by water or energy balance*, 54 (December): 56–65. <https://doi.org/10.1016/j.jtherbio.2014.12.003>.
- Horne, Curtis R., Andrew. G. Hirst, and David Atkinson. 2015. "Temperature-Size Responses Match Latitudinal-Size Clines in Arthropods, Revealing Critical Differences between Aquatic and Terrestrial Species." *Ecology Letters* 18 (4): 327–35. <https://doi.org/10.1111/ele.12413>.
- Johnston, Ian A, Sujatha Manthri, Richard Alderson, Patrick Campbell, David Mitchell, David Whyte, Alistair Dingwall, David Nickell, Craig Selkirk, and Billy Robertson. 2002. "Effects of Dietary Protein

- 644 Level on Muscle Cellularity and Flesh Quality in Atlantic Salmon with Particular Reference to Gaping.”
645 *Aquaculture* 210 (1): 259–83. [https://doi.org/10.1016/S0044-8486\(01\)00862-6](https://doi.org/10.1016/S0044-8486(01)00862-6).
- 646 Kalinkat, Gregor, Florian D. Schneider, Christoph Digel, Christian Guill, Björn C. Rall, and Ulrich Brose.
647 2013. “Body Masses, Functional Responses and Predator–Prey Stability.” *Ecology Letters* 16 (9):
648 1126–34. <https://doi.org/10.1111/ele.12147>.
- 649 Kiełbasa, Anna, Aleksandra Walczyńska, Edyta Fiałkowska, Agnieszka Pajdak-Stós, and Jan Kozłowski.
650 2014. “Seasonal Changes in the Body Size of Two Rotifer Species Living in Activated Sludge Follow the
651 Temperature-Size Rule”. *Ecology and Evolution* 4 (24): 4678–89. <https://doi.org/10.1002/ece3.1292>.
- 652 Kingsolver, JG, and Raymond Huey. 2008. “Size, Temperature, and Fitness: Three Rules.” *Evolutionary*
653 *Ecology Research* 10 (February): 251–68.
- 654 Kingsolver, Joel G., J. Gwen Shlichta, Gregory J. Ragland, and Katie R. Massie. 2006. “Thermal Reac-
655 tion Norms for Caterpillar Growth Depend on Diet.” *Evolutionary Ecology Research* 8 (4): 703–15.
- 656 Koussoroplis, Apostolos-Manuel, and Alexander Wacker. 2016. “Covariance Modulates the Effect of
657 Joint Temperature and Food Variance on Ectotherm Life-History Traits.” *Ecology Letters* 19 (2): 143–
658 52. <https://doi.org/10.1111/ele.12546>.
- 659 Lee, Kwang Pum, and Chris Roh. 2010. “Temperature-by-Nutrient Interactions Affecting Growth Rate
660 in an Insect Ectotherm”. *Entomologia Experimentalis et Applicata* 136 (2): 151–63.
661 <https://doi.org/10.1111/j.1570-7458.2010.01018.x>.
- 662 Lemoine, Nathan P., and Deron E. Burkepile. 2012. “Temperature-Induced Mismatches between Con-
663 sumption and Metabolism Reduce Consumer Fitness.” *Ecology* 93 (11): 2483–89.
664 <https://doi.org/10.1890/12-0375.1>.
- 665 Levin, Sam C., Dylan Z. Childs, Aldo Compagnoni, Sanne Evers, Tiffany M. Knight, and Roberto Sal-
666 guero-Gómez. 2021. “Ipmr: Flexible Implementation of Integral Projection Models in R.” *Methods in*
667 *Ecology and Evolution* 12 (10): 1826–34. <https://doi.org/10.1111/2041-210X.13683>.
- 668 Loisel, Ayala, Alejandro Isla, and Martin Daufresne. 2019. “Variation of Thermal Plasticity in Growth
669 and Reproduction Patterns: Importance of Ancestral and Developmental Temperatures.” *Journal of*
670 *Thermal Biology* 84: 460–68. <https://doi.org/10.1016/j.jtherbio.2019.07.029>.
- 671 Marn, Nina, Marko Jusup, Tarzan Legović, S. A. L. M. Kooijman, and Tin Klanjšček. 2017. “Environ-
672 mental Effects on Growth, Reproduction, and Life-History Traits of Loggerhead Turtles.” *Ecological*
673 *Modelling* 360 (September): 163–78. <https://doi.org/10.1016/j.ecolmodel.2017.07.001>.
- 674 McLeod, Ian M., Jodie L. Rummer, Timothy D. Clark, Geoffrey P. Jones, Mark I. McCormick, Amelia S.
675 Wenger, and Philip L. Munday. 2013. “Climate Change and the Performance of Larval Coral Reef
676 Fishes: The Interaction between Temperature and Food Availability.” *Conservation Physiology* 1 (1).
677 <https://doi.org/10.1093/conphys/cot024>.
- 678 Meyer, Judy L., Michael J. Sale, Patrick J. Mulholland, and N. LeRoy Poff. 1999. “Impacts of Climate
679 Change on Aquatic Ecosystem Functioning and Health1.” *JAWRA Journal of the American Water Re-*
680 *sources Association* 35 (6): 1373–86. <https://doi.org/10.1111/j.1752-1688.1999.tb04222.x>.
- 681 Osmond, Matthew M., Matthew A. Barbour, Joey R. Bernhardt, Matthew W. Pennell, Jennifer M.
682 Sunday, and Mary I. O’Connor. 2017. “Warming-Induced Changes to Body Size Stabilize Consumer-
683 Resource Dynamics.” *The American Naturalist* 189 (6): 718–25. <https://doi.org/10.1086/691387>.

- 684 Paerl, Hans, and Jef Huisman. 2008. "Blooms Like It Hot." *Science (New York, N.Y.)* 320 (May): 57–58.
 685 <https://doi.org/10.1126/science.1155398>.
- 686 Paerl, Hans W. 2014. "Mitigating Harmful Cyanobacterial Blooms in a Human- and Climatically-Im-
 687 pacted World." *Life* 4 (4): 988–1012. <https://doi.org/10.3390/life4040988>.
- 688 Parmesan, Camille, and Gary Yohe. 2003. "A Globally Coherent Fingerprint of Climate Change Im-
 689 pacts across Natural Systems." *Nature* 421 (6918): 37–42. <https://doi.org/10.1038/nature01286>.
- 690 Perrin, N. 1995. "About Berrigan and Charnov's Life-History Puzzle." *Oikos* 73 (1): 137–39.
 691 <https://doi.org/10.2307/3545737>.
- 692 Persson, Jonas, Marcin Włodzimierz Wojewodziec, Dag Olav Hessen, and Tom Andersen. 2011. "In-
 693 creased Risk of Phosphorus Limitation at Higher Temperatures for *Daphnia Magna*." *Oecologia* 165
 694 (1): 123–29. <https://doi.org/10.1007/s00442-010-1756-4>.
- 695 Peters, Robert Henry. 1983. *The Ecological Implications of Body Size*. Cambridge Studies in Ecology.
 696 Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511608551>.
- 697 Pifferi, Fabien, Jérémy Terrien, Julia Marchal, Alexandre Dal-Pan, Fathia Djelti, Isabelle Hardy, Sabine
 698 Chahory, et al. 2018. "Caloric Restriction Increases Lifespan but Affects Brain Integrity in Grey Mouse
 699 Lemur Primates." *Communications Biology* 1 (1): 1–8. <https://doi.org/10.1038/s42003-018-0024-8>.
- 700 Pritchard, Daniel W., Rachel A. Paterson, Helene C. Bovy, and Daniel Barrios-O'Neill. 2017. "Frair: An
 701 R Package for Fitting and Comparing Consumer Functional Responses." *Methods in Ecology and Evo-*
 702 *lution* 8 (11): 1528–34. <https://doi.org/10.1111/2041-210X.12784>.
- 703 Rasmussen, R. S., and T. H. Ostenfeld. 2000. "Influence of Growth Rate on White Muscle Dynamics in
 704 Rainbow Trout and Brook Trout." *Journal of Fish Biology* 56 (6): 1548–52.
 705 <https://doi.org/10.1111/j.1095-8649.2000.tb02164.x>.
- 706 Renner, Susanne S., and Constantin M. Zohner. 2018. "Climate Change and Phenological Mismatch in
 707 Trophic Interactions Among Plants, Insects, and Vertebrates." *Annual Review of Ecology, Evolution,*
 708 *and Systematics* 49 (1): 165–82. <https://doi.org/10.1146/annurev-ecolsys-110617-062535>.
- 709 Rohner, Patrick T., Wolf U. Blanckenhorn, and Martin A. Schäfer. 2017. "Critical Weight Mediates
 710 Sex-Specific Body Size Plasticity and Sexual Dimorphism in the Yellow Dung Fly *Scathophaga Sterco-*
 711 *raria* (Diptera: Scathophagidae)." *Evolution & Development* 19 (3): 147–56.
 712 <https://doi.org/10.1111/ede.12223>.
- 713 Sentis, Arnaud, Amrei Binzer, and David S. Boukal. 2017. "Temperature-Size Responses Alter Food
 714 Chain Persistence across Environmental Gradients." *Ecology Letters* 20 (7): 852–62.
 715 <https://doi.org/10.1111/ele.12779>.
- 716 Sentis, Arnaud, Bart Haegeman, and José M. Montoya. 2022. "Stoichiometric Constraints Modulate
 717 Temperature and Nutrient Effects on Biomass Distribution and Community Stability." *Oikos* 2022 (7).
 718 <https://doi.org/10.1111/oik.08601>.
- 719 Sentis, Arnaud, Jean-Louis Hemptinne, and Jacques Brodeur. 2012. "Using Functional Response Mod-
 720 eling to Investigate the Effect of Temperature on Predator Feeding Rate and Energetic Efficiency."
 721 *Oecologia* 169 (4): 1117–25. <https://doi.org/10.1007/s00442-012-2255-6>.

- 722 Sentis, Arnaud, Jean-Louis Hemptinne, and Jacques Brodeur. 2014. "Towards a Mechanistic Under-
723 standing of Temperature and Enrichment Effects on Species Interaction Strength, Omnivory and
724 Food-Web Structure." *Ecology Letters* 17 (7): 785–93. <https://doi.org/10.1111/ele.12281>.
- 725 Sheridan, Jennifer A., and David Bickford. 2011. "Shrinking Body Size as an Ecological Response to Cli-
726 mate Change." *Nature Climate Change* 1 (8): 401–6. <https://doi.org/10.1038/nclimate1259>.
- 727 Sohal, Rajindar S., and Richard Weindruch. 1996. "Oxidative Stress, Caloric Restriction, and Aging."
728 *Science* 273 (5271): 59–63. <https://doi.org/10.1126/science.273.5271.59>.
- 729 Speakman, John R. 2005. "Body Size, Energy Metabolism and Lifespan." *Journal of Experimental Biol-*
730 *ogy* 208 (9): 1717–30. <https://doi.org/10.1242/jeb.01556>.
- 731 Su, Y. S., Yajima, M., Su, M. Y. S., & SystemRequirements, J. A. G. S. (2015). *Package 'R2jags'*. R package
732 version 0.03-08, URL <http://CRAN.R-project.org/package=R2jags>.
- 733 Therneau T (2022). *A Package for Survival Analysis in R*. R package version 3.3-1, <https://CRAN.R-pro->
734 [ject.org/package=survival](https://CRAN.R-project.org/package=survival).
- 735 Therneau T (2022). *coxme: mixed effects Cox models*. R package version 2.2-18.1, <https://CRAN.R->
736 [project.org/package=coxme](https://CRAN.R-project.org/package=coxme).
- 737 Thierry, B. 2005. "Integrating Proximate and Ultimate Causation: Just One More Go!" *Current Science*
738 89 (7): 1180–83.
- 739 Twining, Cornelia W., J. Ryan Shipley, and Blake Matthews. 2022. "Climate Change Creates Nutri-
740 tional Phenological Mismatches." *Trends in Ecology & Evolution*, July.
741 <https://doi.org/10.1016/j.tree.2022.06.009>.
- 742 Urrutia-Cordero, Pablo, Mattias K. Ekvall, Jens Ratcovich, Margarida Soares, Susanne Wilken, Huan
743 Zhang, and Lars-Anders Hansson. 2017. "Phytoplankton Diversity Loss along a Gradient of Future
744 Warming and Brownification in Freshwater Mesocosms." *Freshwater Biology* 62 (11): 1869–78.
745 <https://doi.org/10.1111/fwb.13027>.
- 746 Uszko, Wojciech, Magnus Huss, and Anna Gårdmark. 2022. "Smaller Species but Larger Stages:
747 Warming Effects on Inter- and Intraspecific Community Size Structure." *Ecology* 103 (7): e3699.
748 <https://doi.org/10.1002/ecy.3699>.
- 749 Vagnon, Chloé, Franck Cattaneo, Chloé Goulon, David Grimardias, Jean Guillard, and Victor Frossard.
750 2021. "An Allometric Niche Model for Species Interactions in Temperate Freshwater Ecosystems."
751 *Ecosphere* 12 (3): e03420. <https://doi.org/10.1002/ecs2.3420>.
- 752 Verberk, Wilco C.E.P., David Atkinson, K. Natan Hoefnagel, Andrew G. Hirst, Curtis R. Horne, and
753 Henk Siepel. 2021. "Shrinking Body Sizes in Response to Warming: Explanations for the Tempera-
754 ture–Size Rule with Special Emphasis on the Role of Oxygen." *Biological Reviews* 96 (1): 247–68.
755 <https://doi.org/10.1111/brv.12653>.
- 756 Visser, Marcel E, and Christiaan Both. 2005. "Shifts in Phenology Due to Global Climate Change: The
757 Need for a Yardstick." *Proceedings of the Royal Society B: Biological Sciences* 272 (1581): 2561–69.
758 <https://doi.org/10.1098/rspb.2005.3356>.
- 759 Visser, Marcel E., Leonard J. M. Holleman, and Phillip Gienapp. 2006. "Shifts in Caterpillar Biomass
760 Phenology Due to Climate Change and Its Impact on the Breeding Biology of an Insectivorous Bird."
761 *Oecologia* 147 (1): 164–72. <https://doi.org/10.1007/s00442-005-0299-6>.

- 762 Walczyńska, Aleksandra, Anna Kiełbasa, and Mateusz Sobczyk. 2016. "'Optimal Thermal Range' in Ec-
763 totherms: Defining Criteria for Tests of the Temperature-Size-Rule." *Journal of Thermal Biology* 60:
764 41–48. <https://doi.org/10.1016/j.jtherbio.2016.06.006>.
- 765 Walczyńska, Aleksandra, Anna Maria Labecka, Mateusz Sobczyk, Marcin Czarnoleski, and Jan
766 Kozłowski. 2015. "The Temperature–Size Rule in Lecane Inermis (Rotifera) Is Adaptive and Driven by
767 Nuclei Size Adjustment to Temperature and Oxygen Combinations". *Journal of Thermal Biology* 54:
768 78–85. <https://doi.org/10.1016/j.jtherbio.2014.11.002>.
- 769 Walczyńska, Aleksandra, and Łukasz Sobczyk. 2017. "The Underestimated Role of Temperature–Oxy-
770 gen Relationship in Large-Scale Studies on Size-to-Temperature Response". *Ecology and Evolution* 7
771 (18): 7434–41. <https://doi.org/10.1002/ece3.3263>.
- 772 Walters, Richard John, and Mark Hassall. 2006. "The Temperature-Size Rule in Ectotherms: May a
773 General Explanation Exist after All?" *The American Naturalist* 167 (4): 510–23.
774 <https://doi.org/10.1086/501029>.
- 775 Williams, Richard J., and Neo D. Martinez. 2000. "Simple Rules Yield Complex Food Webs." *Nature*
776 404 (6774): 180–83. <https://doi.org/10.1038/35004572>.
- 777 Winder, Monika, and Daniel E. Schindler. 2004. "Climate Change Uncouples Trophic Interactions in an
778 Aquatic Ecosystem." *Ecology* 85 (8): 2100–2106. <https://doi.org/10.1890/04-0151>.
- 779 Wojewodzic, Marcin W., Marcia Kyle, James J. Elser, Dag O. Hessen, and Tom Andersen. 2011. "Joint
780 Effect of Phosphorus Limitation and Temperature on Alkaline Phosphatase Activity and Somatic
781 Growth in *Daphnia Magna*." *Oecologia* 165 (4): 837–46. <https://doi.org/10.1007/s00442-010-1863-2>.
- 782 Xia, Qin-Wen, Chao Chen, Jian-Jun Tang, Hai-Min He, and Fang-Sen Xue. 2019. "A Reverse Tempera-
783 ture-Size Rule Associated with a Negative Relationship between Larval Development Time and Pupal
784 Weight in a Tropical Population of *Ostrinia Furnacalis*". *Physiological Entomology* 44 (3-4): 209–14.
785 <https://doi.org/10.1111/phen.12302>.
- 786 Yamamoto, T. 1975. "Medaka (Killifish)". *Biology and Strains* 365.
787 <https://cir.nii.ac.jp/crid/1574231874426383360>.
- 788 Yodzis, P., and S. Innes. 1992. "Body Size and Consumer-Resource Dynamics." *The American Natural-*
789 *ist* 139 (6): 1151–75. <https://doi.org/10.1086/285380>.
- 790 Zamudio, Kelly R., Raymond B. Huey, and Wayne D. Crill. 1995. "Bigger Isn't Always Better: Body Size,
791 Developmental and Parental Temperature and Male Territorial Success in *Drosophila Melanogaster*."
792 *Animal Behaviour* 49 (3): 671–77. [https://doi.org/10.1016/0003-3472\(95\)80200-2](https://doi.org/10.1016/0003-3472(95)80200-2).
- 793 Zuo, Wenyun, Melanie E. Moses, Geoffrey B. West, Chen Hou, and James H. Brown. 2012. "A General
794 Model for Effects of Temperature on Ectotherm Ontogenetic Growth and Development." *Proceed-*
795 *ings of the Royal Society B: Biological Sciences* 279 (1734): 1840–46.
796 <https://doi.org/10.1098/rspb.2011.2000>.

Appendix

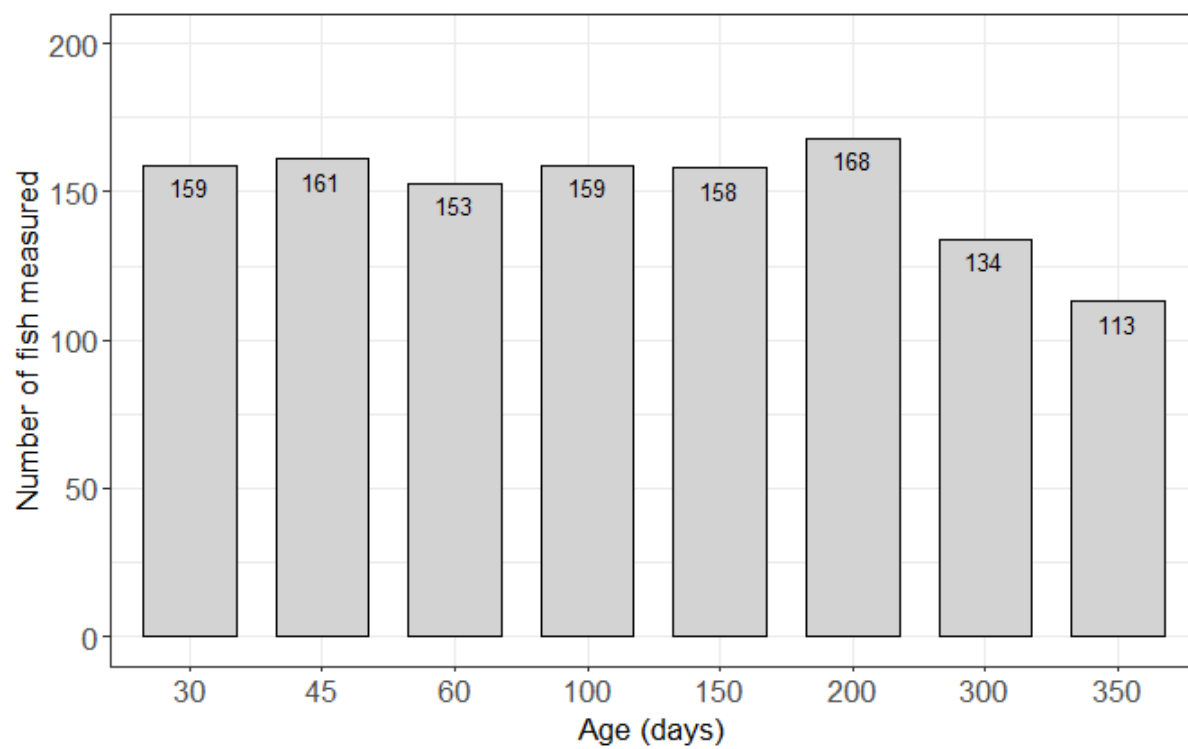


Fig. S 1: Number of fish measured at different ages.

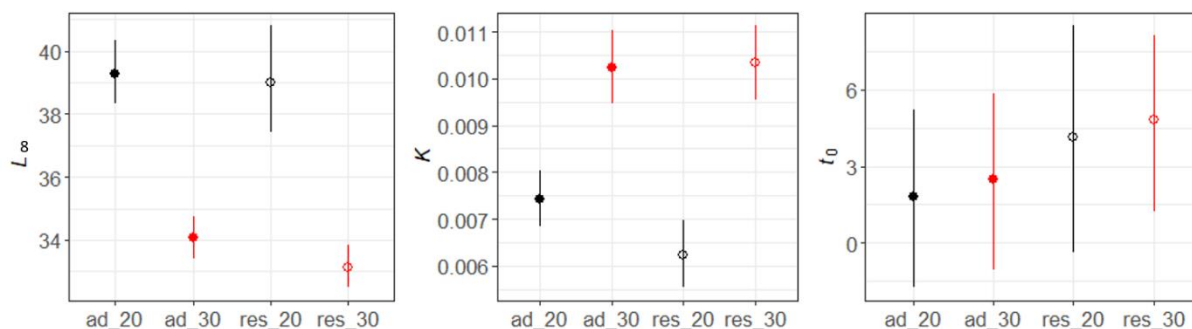


Fig. S 2 : Estimated Von Bertalanffy parameters for each treatment.

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. Bars represent 95 % credibility intervals.

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

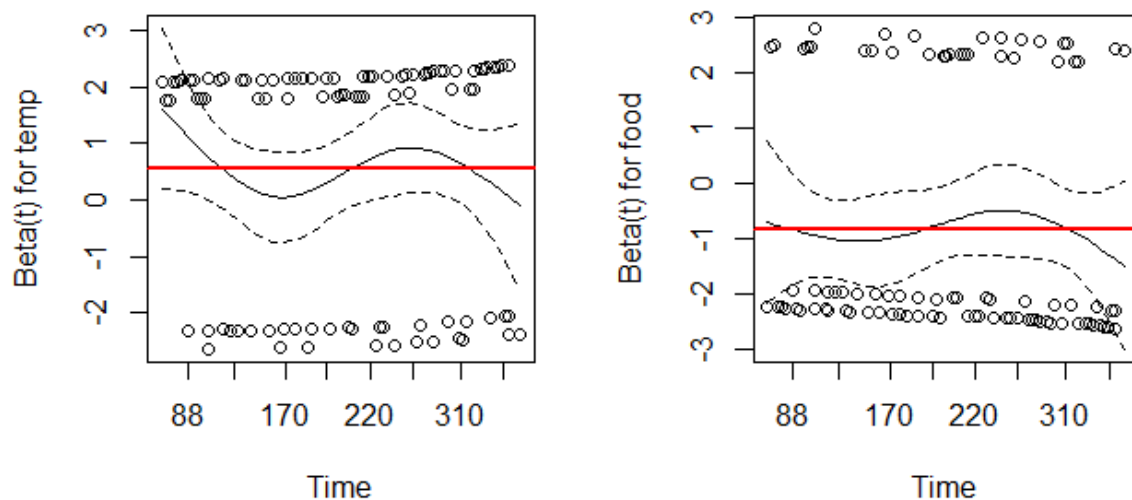


Fig. S 3: Cox model assumption of proportionality for temperature and food condition.

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

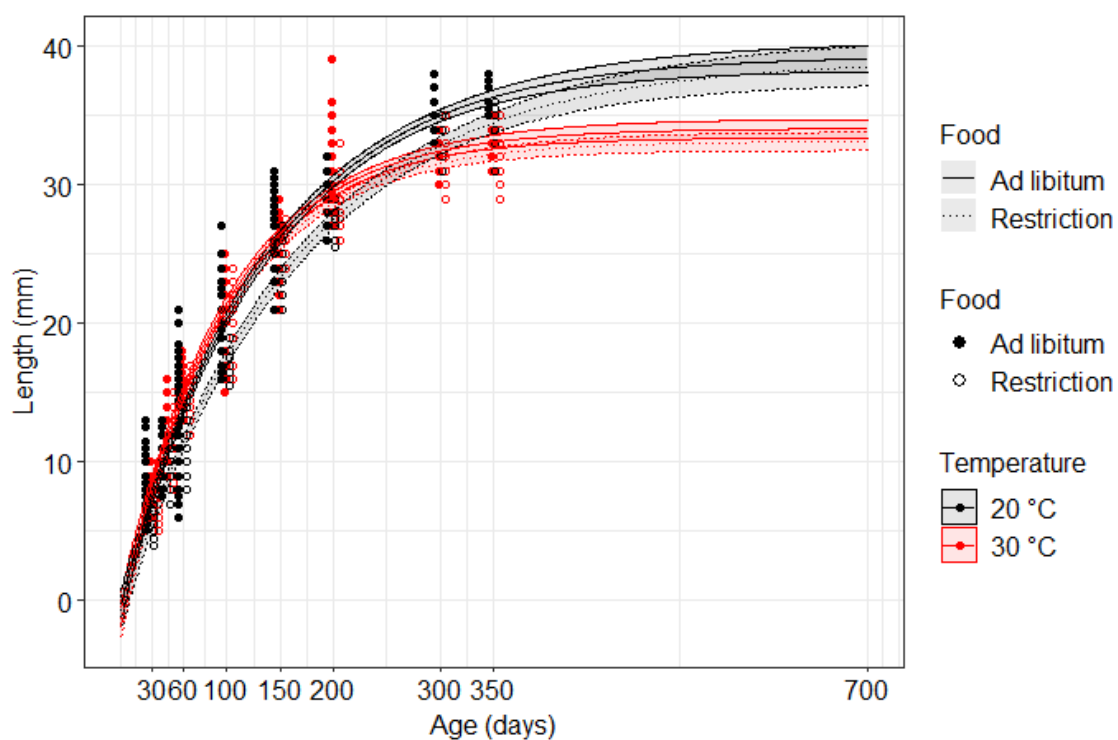


Fig. S 4: Extrapolation of Von Bertalanffy growth curve for each combination of temperature and food conditions.
 Black and red colors represent the cold and warm treatments, respectively. Solid and dotted lines represent the ad libitum and the food restriction treatments, respectively. Areas represent the 95 % credibility intervals.
 Points represent experimentally measured sizes at age.

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

Reference	Variable	Size at maturity	Adult size
Betini <i>et al.</i> (2020)	Warming	x	-
	Food	x	+
Courtney-Jones <i>et al.</i> (2015)	Warming	-	
	Food	-	
Giberson and Rosenberg (1992)	Warming		+
	Food		+
Giebelhausen and Lampert (2001)	Warming	-	
	Food	-	
Kielbasa <i>et al.</i> (2014)	Warming		
	Food		
	Interaction		Adult size reduction with only 1 of 2 nutritional qualities
Lee and Roh (2010)	Warming		
	Food		
	Interaction	Mass at pupation reduction under extreme food conditions	
Marn <i>et al.</i> (2017)	Warming	x	x
	Food	x	+
McLeod <i>et al.</i> (2013)	Warming	x	
	Food	x	
Rohner <i>et al.</i> (2017)	Warming	x	
	Food	-	

830

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

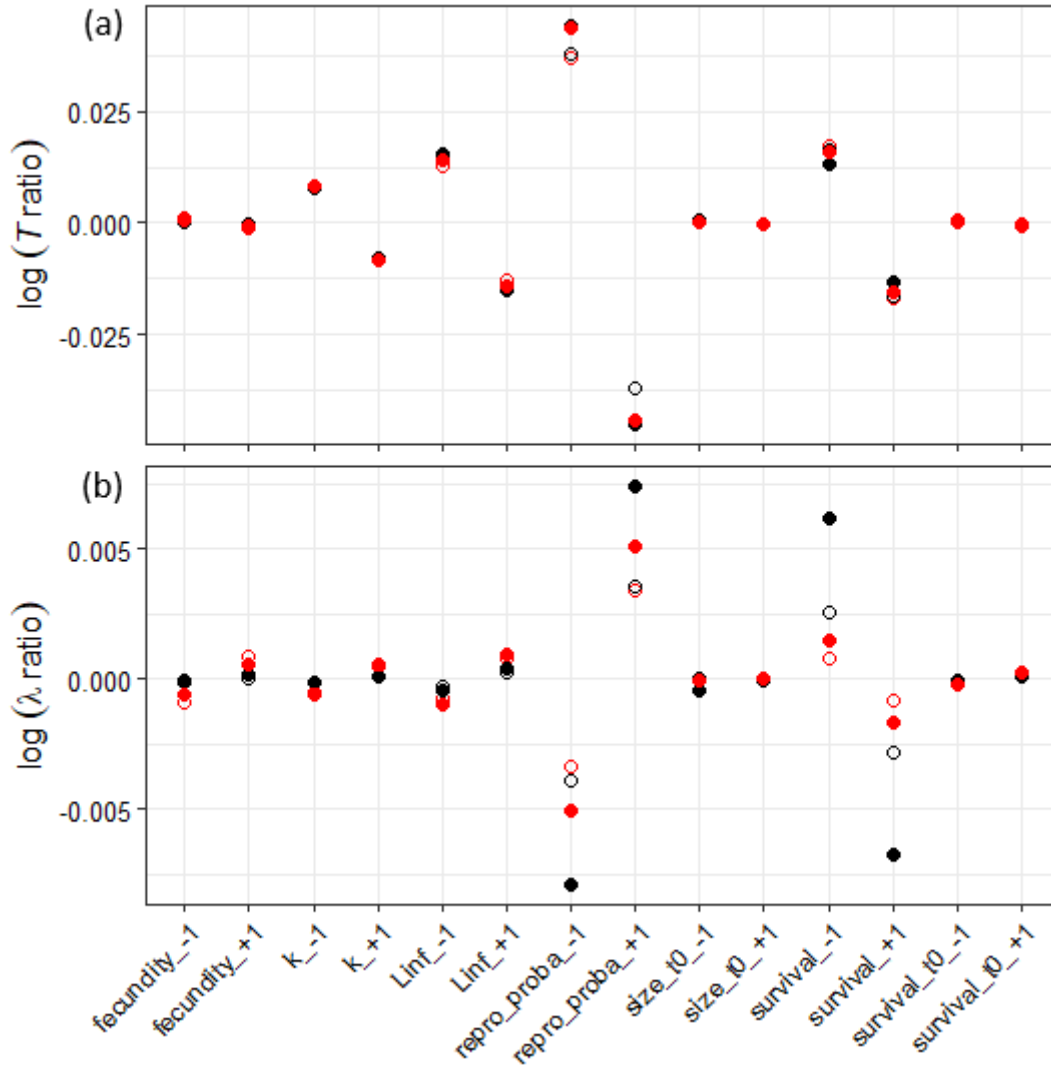


Fig. S 5: Sensitivity analysis of (a) generation time T and (b) asymptotic per capita population growth rate λ . Black and red colors correspond to the cold and warm treatments, respectively. Filled and empty circles correspond to the median of ad libitum and food restriction treatments, respectively.

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 (Fig. S 5). 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, 10.3, 2.4, and 1.8 days for conditions ad_20, res_20, ad_30, and res_30, respectively. Not surprisingly, this input strongly influences the demographic parameters since in the model the length of time a fish is fertile depends directly on age at maturity. Demographic parameters are also sensitive

854 to the probability of survival. As with the probability of reproduction, this survival probability also
855 determines the length of time a fish can produce eggs before it dies. Finally, the generation time is
856 somewhat sensitive to the K and L_{∞} parameters of the Von Bertalanffy model. By influencing growth,
857 these parameters will determine the rate at which a fish reaches size at sexual maturity in the model,
858 and thus the rate at which a fish can reproduce, directly impacting generation time.