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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

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

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

46 Introduction

47

48 Body size reduction has been proposed as a third universal species response to global warming
49 (Daufresne *et al.* 2009, Gardner *et al.* 2011, Sheridan and Bickford 2011), in addition to changes in
50 phenology (Visser and Both 2005) and geographic distribution (Parmesan and Yohe 2003). While the
51 first two responses have been studied extensively (Meyer *et al.* 1999), the third one has received less
52 attention despite its high prevalence and magnitude. For instance, body size can reduce up to -4 %
53 per °C in terrestrial species and up to -8 % per °C in aquatic ectotherms (Forster *et al.* 2012). Previous
54 studies focused on proximal mechanisms, (i.e. how environmental factors influence life history traits
55 by impacting physiological and developmental processes (Thierry 2005)) and ultimate mechanisms
56 related to the evolution and adaptive value of body size changes (Zuo *et al.* 2012, Atkinson and Sibly
57 1997, Frazier *et al.* 2001, Hoefnagel and Verberk 2015, Walczyńska *et al.* 2015, Verberk *et al.* 2021)
58 and their variability among species and habitats (Horne *et al.* 2015, Forster *et al.* 2012, Atkinson 1994).
59 In aquatic systems, warming decreases oxygen concentration and hypoxia tends to amplify TS
60 responses, which has been interpreted as a response to limited oxygen resource (Frazier *et al.* 2001,
61 Hoefnagel and Verberk 2015, Verberk *et al.* 2021). In contrast, in terrestrial system, oxygen is less
62 limiting and other factors may be more important than oxygen concentration. For instance, the risks
63 of not completing juvenile development in time before the onset of winter strongly determine growth
64 pattern in terrestrial organisms whereas it has less influence in the growth of aquatic organisms
65 (Verberk *et al.* 2021). These differences may explain why TS responses are weaker in terrestrial than
66 in aquatic ecosystems (Forster *et al.* 2012). At the individual level, body size shift can be explained by
67 the "Temperature Size Rule" (TSR, Atkinson 1994, Atkinson and Sibly 1997, Angilletta *et al.* 2004,
68 Berrigan and Charnov 1994, Perrin 1995, Arendt 2007, Arendt 2011), which states that ectotherms
69 grow faster but reach a smaller size at a given stage of development (e.g. size at maturity or adult size)
70 under warm environment compared to colder ones, resulting in "crossed" growth curves (Figure 1).
71 This pattern of TSR remains an evolutionary puzzle (Atkinson and Sibly 1997) and body size shifts could
72 be the result of different developmental strategies. For example, a recent study showed that warming
73 accelerates growth and reproduction leading to a rapid life cycle but also a decrease in adult survival
74 in a temperate lizard species (Bestion *et al.* 2015). This study and others (Marn *et al.* 2017, Courtney
75 Jones *et al.* 2015, Corrêa *et al.* 2021, Clissold and Simpson 2015, Kingsolver *et al.* 2006, Rohner *et al.*
76 2017) suggest that it is important to investigate the links between growth trajectories and fitness
77 related traits (survival and fecundity) to better understand the underlying trade-offs and how the
78 combination of these traits may influence individual fitness and population demographic parameters.
79 However, most studies on TSR did not investigate these links (but see Marn *et al.* 2017, Corrêa *et al.*
80 2021, Kingsolver *et al.* 2006) which limits our ability to detect situations in which TSR might be adaptive
81 (i.e. increase fitness) or maladaptive.

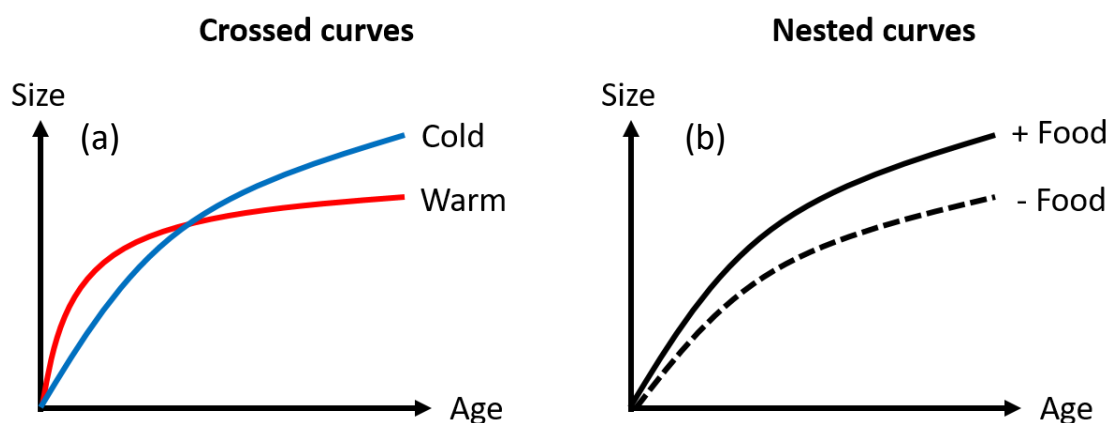
82 Besides temperature, another major factor underlying growth, reproduction and survival is
83 food availability (Boggs and Ross 1993, Giberson and Rosenberg 1992, Boersma and Vijverberg 1996,
84 Corrêa *et al.* 2021). Individuals need enough resources, as energy and material inputs, to sustain their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

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

124 In this study, we address this gap by experimentally investigating growth, reproduction and
125 survival probability of a vertebrate predatory species, the medaka fish (*Oryzias latipes*, Temminck &

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

141



142

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

145

146 Material and methods

147 Biological system and rearing conditions

148

149 The medaka is a small iteroparous freshwater fish native to East Asia (Hirshfield 1980). The life
 150 span of a medaka is about 2 years and its adult size varies between 30 and 50 mm (Ding *et al.* 2010,
 151 Egami and Etoh, 1969). This is an eurythermal species (5 °C - 35 °C) with an optimum temperature of
 152 25 °C (Dhillon and Fox 2004). At this temperature, the medaka requires only 10 to 12 weeks to reach
 153 sexual maturity. Fish were maintained in the laboratory using an open water system with water supply
 154 controlled by drip emitters (1 L.h⁻¹). Input water quality was maintained with mechanical, biological
 155 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
 156 to prevent high nitrite concentrations and maintain oxygen at saturation.

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

166 From this F₀ generation, about 300 eggs were collected in each tank. Eggs were placed in small
167 nurseries (2.5 L) made of fine mesh and each nursery was placed in the tank where the eggs were
168 collected from (see Hemmer-Brepson *et al.* 2014, Loisel *et al.* 2019 for more details). After 30 days of
169 growth, the parents were removed and the F₁ fish larvae were reared under four different treatment:
170 ad_20 (*ad libitum* and 20 °C), res_20 (restriction and 20 °C), ad_30 (*ad libitum* and 30 °C) and res_30
171 (restriction and 30 °C). For each treatment, the growth of approximately 80 fish was monitored, except
172 for res_20 where only 54 fish could be maintained. Fish were maintained in 20 L aquaria with 20 - 30
173 fish of a single treatment. This density (less than 2 - 3 fish per liter) does not cause any stress or
174 agonistic behaviour in this species (Denny *et al.* 1991). The fish were fed with TetraMin[®] (composition:
175 47 % protein, 10 % fat content, 3 % cellulose and 6 % water) every morning (for the *ad libitum*
176 condition) or every two mornings (for the restriction condition). On each feeding days, TetraMin[®] was
177 provided to each tank until the fish no longer went up to the surface to get food. Excess food was
178 systematically removed after feeding to prevent feeding between two meals. Apart from temperature
179 and food, all the experimental parameters were similar in the four treatments.

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

190

191 Growth, fecundity and survival

192

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

200 laid per female per day in each tank. The survival probability from 60 days (age of first sexually mature
201 fish), referred to as survival in this study, was monitored daily until the end of the experiment.

202 Statistical analysis

203

204 TL measurements and ages were used to fit von Bertalanffy growth curve model (Von Berta-
205 lanffy 1938):

$$206 \quad L_t = L_\infty(1 - e^{-K(t-t_0)}) \text{ (eq. 1)}$$

207 Where L_t is the estimated total length at time t , L_∞ the maximum asymptotic size (i.e. the total length
208 for fish with an ∞ age), K the initial growth rate, and t_0 the theoretical age at which body size is null.

209 Von Bertalanffy growth curves parameters (L_∞ , K , t_0) were estimated by Bayesian inference using the
210 Bayesian software JAGS and the "R2jags" package (Su and Yajima, 2015) in R software (version 4.0.2;
211 R development Core Team). We assumed that the asymptotic size L_∞ , the initial growth rate K , and the
212 theoretical age at null size t_0 could vary between temperature (T) and resource (C) condition.
213 Consequently, four values of L_∞ , K and t_0 (one for each combination (CT) of temperature and resource
214 condition) were fitted. For each parameter, we used a normal uninformative prior with a mean of 0
215 and a precision parameter (inverse of the variance) of 0.001:

$$216 \quad L_{\infty CT} \sim N(0, 0.001) \quad K_{CT} \sim N(0, 0.0001) \quad t_{0 CT} \sim N(0, 0.001) \quad \text{(eq. 2)}$$

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

$$219 \quad \begin{vmatrix} \sigma_{L_\infty}^2 & r_1 \cdot \sigma_{L_\infty} \cdot \sigma_K & r_2 \cdot \sigma_{L_\infty} \cdot \sigma_{t_0} \\ r_1 \cdot \sigma_{L_\infty} \cdot \sigma_K & \sigma_K^2 & r_3 \cdot \sigma_K \cdot \sigma_{t_0} \\ r_2 \cdot \sigma_{L_\infty} \cdot \sigma_{t_0} & r_3 \cdot \sigma_K \cdot \sigma_{t_0} & \sigma_{t_0}^2 \end{vmatrix} \text{ (eq. 3)}$$

220 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
221 correlations between these vectors. We used uninformative priors with a uniform distribution for each
222 parameter of Σ , adapting the limits to the parameters (e.g between -1 and 1 for a correlation).

223 $L_{\infty CT}$, K_{CT} and $t_{0 CT}$ are thus hyperpriors (population parameters) that serve to assess parameters for
224 each tank (t) when associated with the random effects. For instance for the L_∞ parameter:

$$225 \quad L_{\infty t} = L_{\infty CT} + \varepsilon_{L_{\infty t}} \text{ (eq. 4)}$$

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

$$228 \quad L_{tj} = L_{\infty t} \left(1 - e^{-K_t(t_j - t_{0t})}\right) \text{ (eq. 5)}$$

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

$$230 \quad \begin{aligned} L_{ftj} &\sim N(L_{tj}, \sigma) \text{ (eq. 6)} \\ \sigma &\sim U(0, 10) \end{aligned}$$

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

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

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

251

252 Integral Projection Modelling

253

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

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

$$267 \quad n(z', t + 1) = \int_L^U K(z', z)n(z, t)dz \text{ (eq. 7)}$$

268 Where $n(z', t+1)$ is the size of the population at time $t+1$, z' is the state variable describing the
 269 population (i.e. body size in our model). $n(z', t+1)$ is obtained by integrating the product of $K(z', z)$ and
 270 $n(z, t)$ over the domain $[L, U]$. In our model, the lower bound L is the minimum fish size and the upper
 271 bound U is the maximum size. $K(z', z)$ is a bivariate kernel function that describes the transitions to state
 272 z' given the initial state of an individual z at time t . $K(z', z)$ consists of two sub-kernels P and F . P
 273 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.

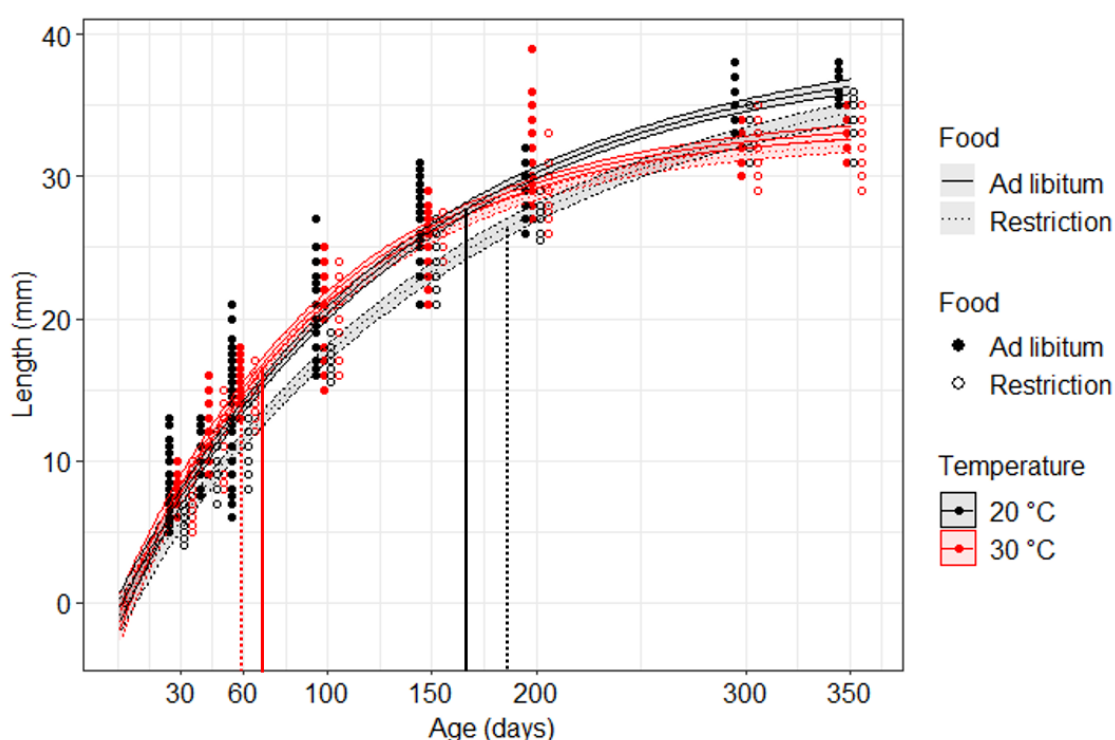
313

314 Results

315

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

324



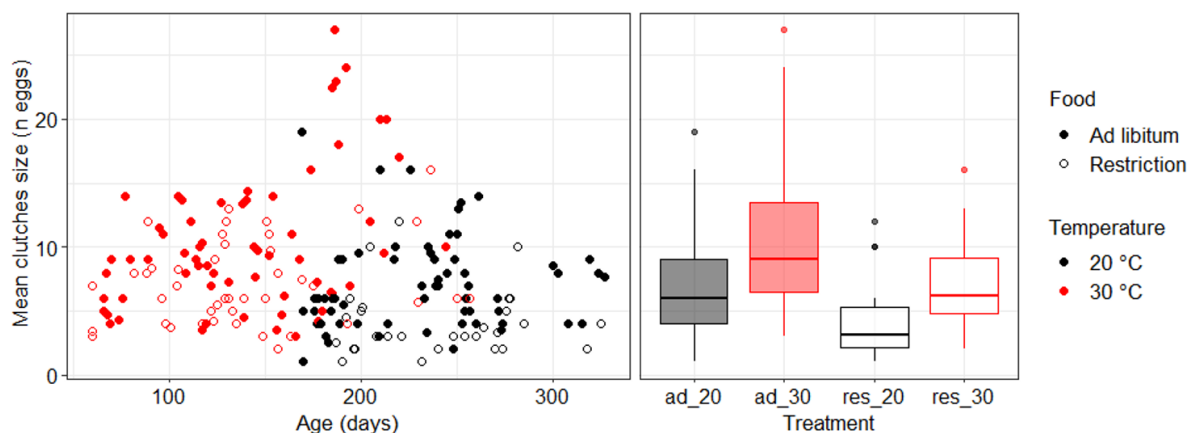
325

326 **Figure 2: Fitted von Bertalanffy growth curve for each combination of temperature and food conditions.**

327 *Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively. Solid and dotted lines*
 328 *represent the ad libitum and the food restriction treatments, respectively. Areas represent the 95 % credibility intervals.*
 329 *Vertical bars represent age at maturity. As fish were not identified individually, jittered points represent experimentally*
 330 *measured sizes (in mm) at age (in days) of fish from different replicates (i.e.tanks).*

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332 In the warm treatment, the fish were sexually mature at 67.3 ± 2.3 days (body length: $16.8 \pm$
 333 0.1 mm) under *ad libitum* condition and at 60 days for all replicates (body length: 17.2 ± 0.7 mm) under
 334 food restriction. In the cold treatment, they were sexually mature at 169.7 ± 0.6 days (body length:
 335 26.3 ± 0.6 mm) and 186.5 ± 0.7 days (body length: 25.7 ± 0.4 mm) under *ad libitum* and food restriction
 336 conditions, respectively (Figure 3). We found that warming increased mean daily clutch size per female
 337 ($df = 1$, $Chi^2 = 13.26$, $p < 0.001$) and food restriction decreased it ($df = 1$, $Chi^2 = 10.58$,
 338 $p = 0.001$). Mean daily clutch size per female was not dependent on the interaction between
 339 temperature and food conditions ($df = 1$, $chi^2 = 0.79$, $p = 0.37$).



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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.

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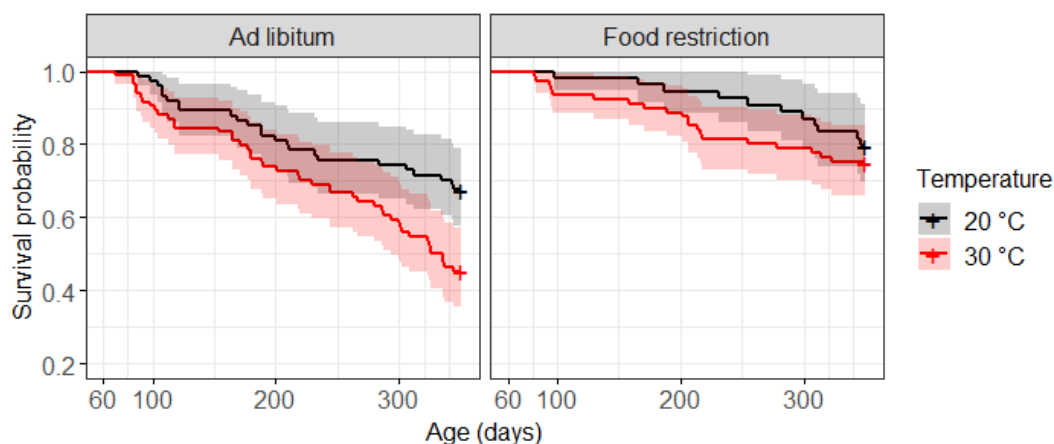
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The fish survival was not significantly affected by the interaction between warming and food restriction ($Chi^2 = 0.70$, $df = 1$, $p = 0.40$, $n = 292$). In contrast, warming significantly reduced the fish survival ($Chi^2 = 6.96$, $df = 1$, $p =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

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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.

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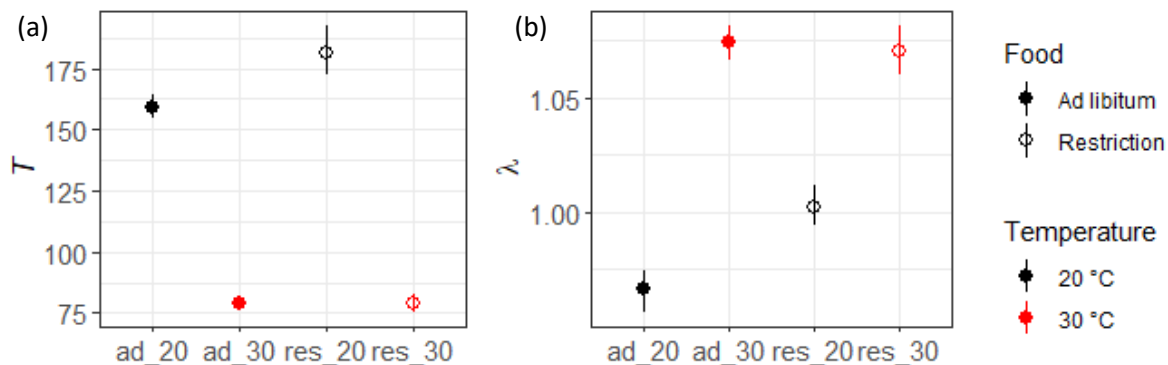
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We found that warming decreased generation time T and increased the asymptotic *per capita* population growth rate λ (Figure 5). In the cold treatment, food restriction significantly increased T and λ . Food restriction had no significant effect on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

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

364 *Black and red colors correspond to the cold and warm treatments, respectively. Filled and empty circles correspond to the*
 365 *median of ad libitum and food restriction treatments, respectively. Bars represent 95 % confident intervals.*

366

367 Discussion

368

369 Shrinking body size with increasing temperature has been proposed as a third universal
 370 response to global warming (Daufresne *et al.* 2009, Gardner *et al.* 2011). In addition, resources are
 371 expected to change with global warming (De Senerpont Domis *et al.* 2014), in response to changes in
 372 physicochemical, phenological (Visser and Both, 2005) and geographical parameters (Parmesan and
 373 Yohe, 2003). The independent and interactive effects of temperature and food availability on life
 374 history traits have been mainly studied in small aquatic (Betini *et al.* 2020, Giebelhausen and Lampert
 375 2001, Wojewodzic *et al.* 2011, Persson *et al.* 2011, Giberson and Rosenberg 1992) and terrestrial
 376 (Clissold and Simpson 2015, Corrêa *et al.* 2021, Rohner *et al.* 2017, Lee and Roh 2010) invertebrate
 377 species. However, we have limited information on how temperature and food availability jointly
 378 influence life history traits in vertebrate predators and how the integration of these traits may
 379 influence population fitness. Our objective was thus to test whether food availability can modulate the
 380 effects of temperature on size at age and life history traits of a vertebrate predator species, the medaka
 381 fish, and to investigate how these traits can affect population demographic parameters and life history
 382 strategies.

383 The results of our laboratory experiment indicate that, in agreement with the TSR rule
 384 (Atkinson and Sibly 1997, Berrigan and Charnov 1994, Arendt 2011), warming leads to crossed growth
 385 curves with individuals growing faster but reaching a smaller size at maturity and adult size compared
 386 to the cold condition. We conducted a short synthesis of the results of previous experimental studies
 387 investigating the responses in size at maturity or adult size to warming and food conditions (see Table
 388 S 1). This synthesis shows the important variability in the responses of size at maturity or adult size to
 389 temperature and food and the complexity of understanding the mechanisms underlying the control of
 390 body size in ectotherms. In line with our results, warming generally leads to a decrease in size at
 391 maturity and adult size in experimental studies (Table S 1). Nevertheless, some studies reported that
 392 temperature does not affect size at maturity or adult size, or can even increase body size (Table S 1).
 393 We found that food restriction does not affect size at maturity but leads to nested curves where
 394 restricted fish are smaller than non-restricted fish for each given age. These results are consistent with
 395 other experimental studies reporting that food restriction decreases adult size but does not affect size

396 at maturity (Table S 1). In contrast, Giebelhausen and Lampert (2001), Courtney Jones *et al.* (2015),
397 and Rohner *et al.* (2017) found a decrease in size at maturity under food restriction. Furthermore, the
398 food restriction effects appeared to be greater at 20 °C where the growth curve for the restricted fish
399 was more nested (i.e. below the curves for non-restricted fish) than at 30 °C. This is surprising because
400 we expected food restriction to have more effect in warm treatment (as reported in McLeod *et al.*
401 2013, Wojewodzic *et al.* 2011, and Persson *et al.* 2011, Giberson and Rosenberg 1992) because
402 warming increases metabolic rates which implies higher energy demand and feeding rate to sustain
403 high metabolic costs (Brown *et al.* 2004). For instance, Betini *et al.* (2020) found a TSR amplification
404 under food restriction with a body size reduction under warming five time stronger under food
405 restriction than under unlimited food conditions. Wojewodzic *et al.* (2011) and Persson *et al.* (2011)
406 also reported that warming further amplifies the decrease in somatic growth rates of *Daphnia* under
407 low nutritional quality (high C:P ratio) compared to *Daphnia* under high nutritional quality (low C:P
408 ratio). These results suggest that temperature-induced body size shifts depend on the quantity but
409 also the quality of resources with lower resource quality amplifying the detrimental effect of warming
410 as reported in a recent study (Sentis *et al.* 2022). In addition to temperature and food, oxygen also
411 appears to be a key factor controlling body size. In particular, TSR tends to be amplified under oxygen
412 limitation (Frazier *et al.* 2001, Hoefnagel and Verberk 2015, Verberk *et al.* 2021). One of the most
413 important differences between oxygen and food availability is that the former generally decreases with
414 increasing temperature, while the latter may increase or decrease with warming. Walczyńska and
415 Sobczyk (2017) suggested that TSR is a plastic response to temperature-dependent oxygen availability,
416 but that food conditions should be controlled as a factor that shapes the strength of TSR.

417 For several species, warming leads to early maturation and increased fecundity (Betini *et al.*
418 2020, Marn *et al.* 2017, Giebelhausen and Lampert 2001). Our results are in line with these studies as
419 we found that fish reared at 30 °C were sexually mature at a younger age and produced a larger mean
420 daily clutch size per female. In contrast, less is known about the responses of developmental rates and
421 fecundity to covariation between temperature and food. Our results did not suggest any effect of food
422 restriction on age at maturity, in contrast to Betini *et al.* (2020) and Marn *et al.* (2017), who found that
423 increased food availability resulted in earlier maturation. However, we found that food restriction
424 decreased mean daily clutch size at both temperature conditions. Several studies have also found that
425 increased food availability increased fecundity in both aquatic (Betini *et al.* 2020, Giberson and
426 Rosenberg 1992) and terrestrial (Corrêa *et al.* 2021) organisms. This can be explained by an increase
427 in the amount of energy to be allocated to reproduction under unlimited food conditions.

428 In addition, the survival probability in our experiment was influenced by both temperature and
429 food restriction. Indeed, fish reared at 30 °C had a lower survival than fish reared at 20 °C while food
430 restriction increased the survival under both temperature conditions. This beneficial effect of food
431 restriction on survival was also observed in frog larvae (Courtney Jones *et al.* 2015) and daphnia (Betini
432 *et al.* 2020). Lower food availability implies a decrease in metabolism and thus a lower production of
433 oxidizing agents which contributes to slow down senescence and increase survival, resulting in a “eat
434 little die old” strategy (Sohal and Weindruch, 1996, Gredilla *et al.* 2001, Speakman 2005, Pifferi *et al.*
435 2018). Our results potentially illustrates different developmental strategies. For example, at 30 °C, fish
436 may have maintained a high growth rate despite food restriction in order to maintain a rapid life cycle,
437 at the expense of lower survival. This hypothesis is supported by the fact that mortality was higher and
438 sexual maturity was reached at a younger age and smaller size at 30 °C compared to 20 °C. Ultimately,
439 measuring the fitness of the fish under the different conditions would help understanding if these

440 strategies are adaptive or results from physiological constraints than are difficulty overpassed by
441 evolutionary adaptations.

442 Although food restriction decreased the mean daily clutch size, these effects were relatively
443 weak compared to the increase in survival. This may be explained by potential acclimation of medaka
444 to rearing temperatures or by food restriction being not severe enough. Reducing feeding events by half
445 (1 out of 2 mornings) was considered restrictive although we cannot exclude compensatory
446 mechanisms were restricted fish would feed more when they have access to food. Although this
447 remains to be investigated in more details, our results highlight the importance of considering the
448 interactions between temperature, body size and food to understand how larger predatory species
449 respond to global changes in terms of developmental and life history strategies. When we integrated
450 our experimentally measured traits into integral projection models (IPM), we found a reduction in
451 generation time and an increase in the population growth rate under warming. Although survival
452 probability was lower under warming, fish reached sexual maturity much faster and had higher
453 fecundity. The earlier sexual maturity of fish enabled them to reproduce for a longer time. Therefore,
454 each female could produce a higher number of juveniles, which leads to a higher population growth
455 rate compared to cold-acclimated populations. Consistent with our experimental data, the IPMs
456 revealed that food restriction had a greater impact on the generation time and growth rate of cold-
457 acclimated populations compared to warm-acclimated populations. Specifically, food restriction
458 increased generation time and asymptotic *per capita* population growth rate at 20 °C, whereas it had
459 no significant effect on demographic parameters of the populations at 30 °C. Our experimental results
460 showed that food restriction slightly decreased fecundity but strongly increased fish survival
461 probability, resulting in longer individual lifespans and the production of more juveniles. Ultimately,
462 food restriction proved evolutionarily advantageous in the cold treatment, leading to a population
463 growth rate equals to unity ($\lambda = 1$). This indicates that the population moves from a declining dynamic
464 ($\lambda < 1$) when food is not limiting to an increasing dynamic ($\lambda > 1$) under food restriction. Our sensitivity
465 analyses revealed that the demographic parameters were mainly sensitive to the reproduction and
466 survival probabilities (see Fig. S 5). These parameters determine the lifespan of the fish and the
467 duration of their reproduction. The high sensitivity of the model to the reproduction probability can
468 be explained by our assumption that, in the model, all females reproduce once they reach maturity
469 (because lacked information on which female reproduces when) which lead to a steep reproduction
470 function. Nevertheless, this assumption was similar for the four treatment and should not influence
471 the qualitative comparison of our four treatments. Overall, IPMs allowed for the combination of traits
472 and confirmed that population mean fitness increases with temperature, and that food restriction
473 increases mean fitness at low temperature.

474 The ecological consequences of temperature-induced changes in body size are multiple. For
475 instance, it can alter predator-prey size ratio which has important implications for the occurrence and
476 strength of predator-prey interactions and thus for community dynamics and food web structure
477 (Sentis *et al.* 2017, Yodzis and Innes 1992, Kalinkat *et al.* 2013, Vagnon *et al.* 2021, Emmerson and
478 Raffaelli 2004, Williams and Martinez 2000). Size interacts with temperature because temperature
479 alters the energetic demands of organisms. For example, higher temperatures can increase short-term
480 predator-prey interaction strength and predator energetic efficiency (Sentis *et al.* 2012). To date,
481 studies examining the consequences of temperature-induced body size shifts on trophic interactions,
482 community dynamics, and food web structure, only considered the reduction in adult size (Sentis *et al.*
483 2017, Osmond *et al.* 2017, Bideault *et al.* 2019). However, our results emphasize the importance of
484 considering ontogeny in future studies as the temperature effect on growth are dependent on life
485 stages. In addition, we expect phenological and geographic changes to alter the quantity and quality

486 of resources (Winder and Schindler 2004, Paerl and Huisman 2008, Paerl 2014, Ekvall *et al.* 2013,
 487 Urrutia-Cordero *et al.* 2017), for example in predator-prey relationships by inducing temporal or spatial
 488 mismatches where the predator is left with reduced food availability (Boukal *et al.* 2019, Twining *et al.*
 489 2022). Along the same line, Visser *et al.* (2006) showed that asynchrony between caterpillar biomass
 490 and the offspring feeding requirements of an insectivorous bird affected the number and weight of
 491 fledged birds. These phenological asynchronies can alter the structure and dynamics of food webs and
 492 modify ecosystem processes (Damien and Tougeron 2019, Renner and Zohner 2018). Altogether, these
 493 studies indicate that it is important to investigate the direct effects of temperature as well as indirect
 494 effects such as altered food quality and availability to better understand the impact of climate change
 495 on growth, survival and fecundity.

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500 Data, scripts and codes availability

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

502 Conflict of interest disclosure

503 The authors of this preprint declare that they have no financial conflict of interest with the content of
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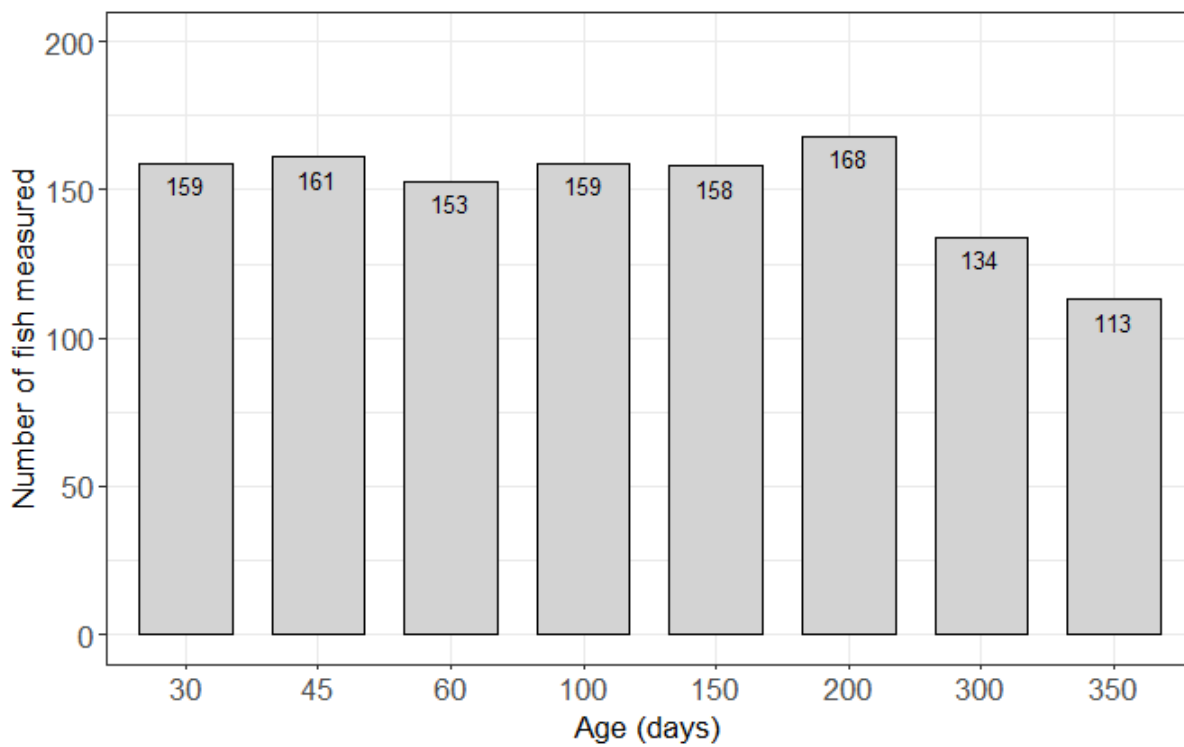
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797 Appendix

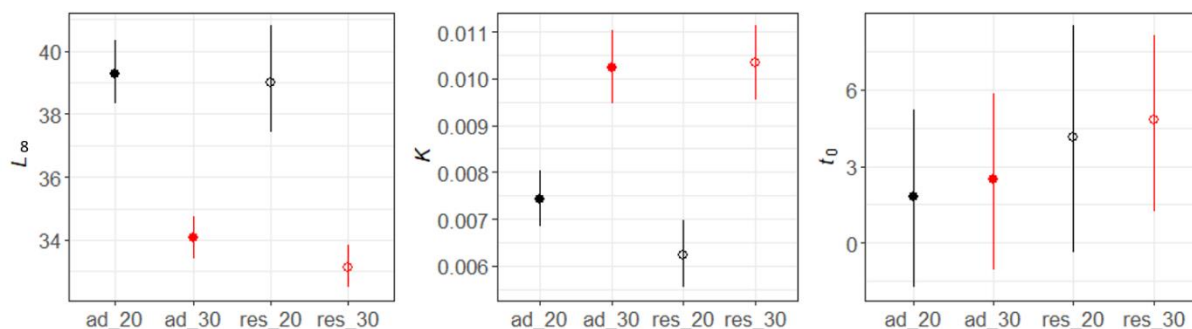
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Fig. S 1: Number of fish measured at different ages.



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Fig. S 2 : Estimated Von Bertalanfy 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.

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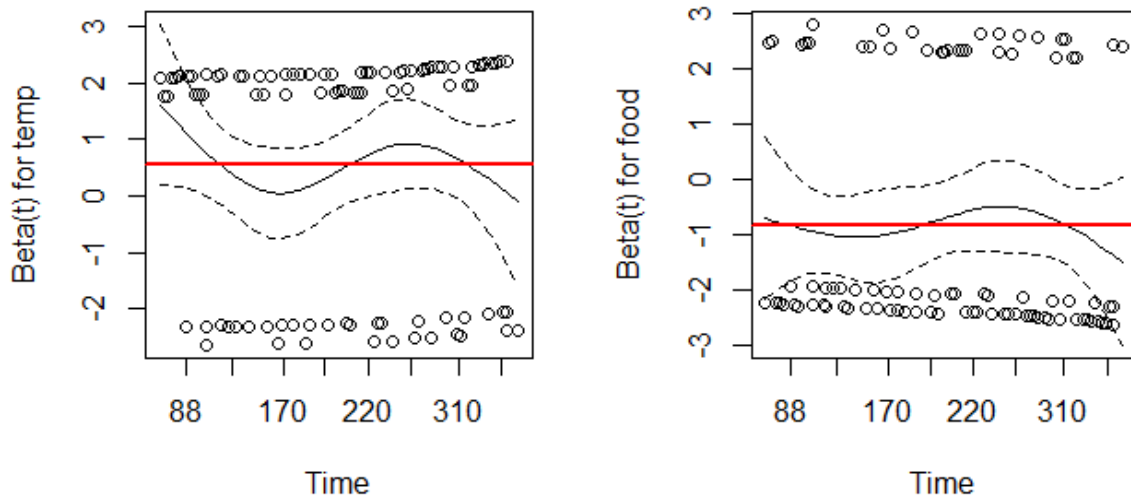
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Consistent with the experimental curves and TSR, warming significantly increased the initial growth rate K and decreased the maximum asymptotic size L_{∞} . Food restriction had no effect on the initial growth rate K for fish reared at 30 °C, but significantly 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.



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

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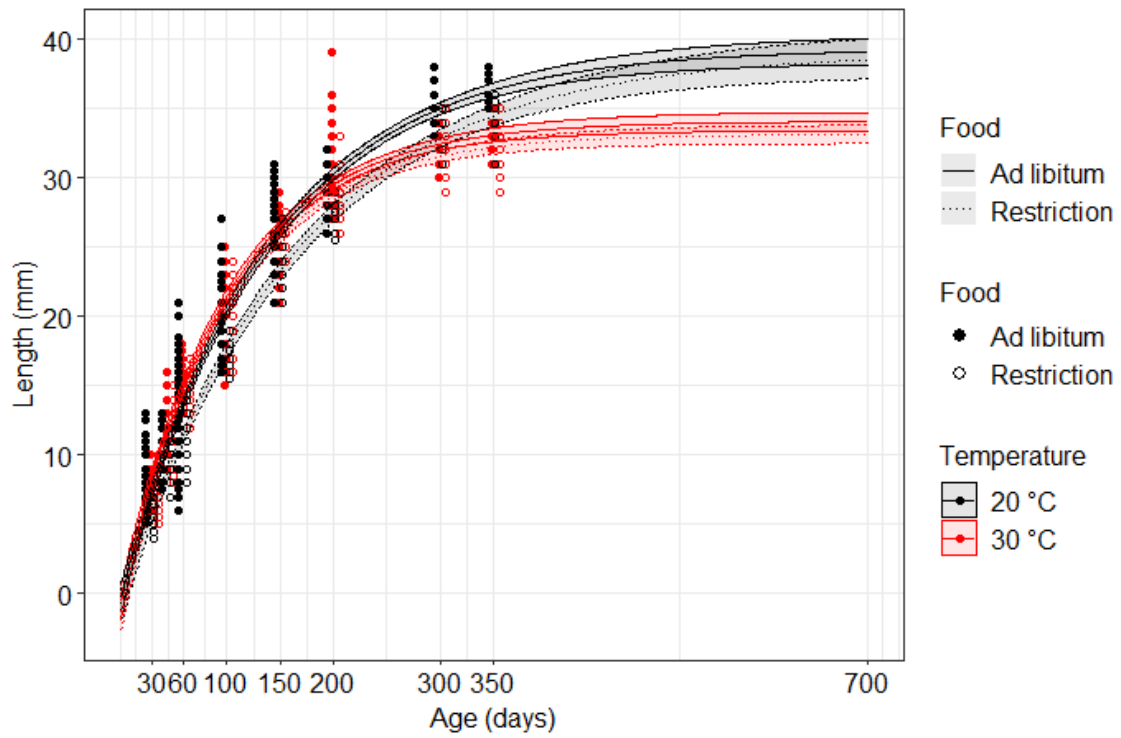
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The *cox.zph* function correlates the scaled Schoenfeld residuals with time for each covariate to test for independence between residuals and time. Additionally, it performs a global test for the model as a whole. From our model output, this test was 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.



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Fig. S 4: Extrapolation of Von Bertalanffy growth curve for each combination of temperature and food conditions.

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Black and red colors represent the cold and warm treatments, respectively. Solid and dotted lines represent the ad libitum

825

and the food restriction treatments, respectively. Areas represent the 95 % credibility intervals.

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Points represent experimentally measured sizes at age.

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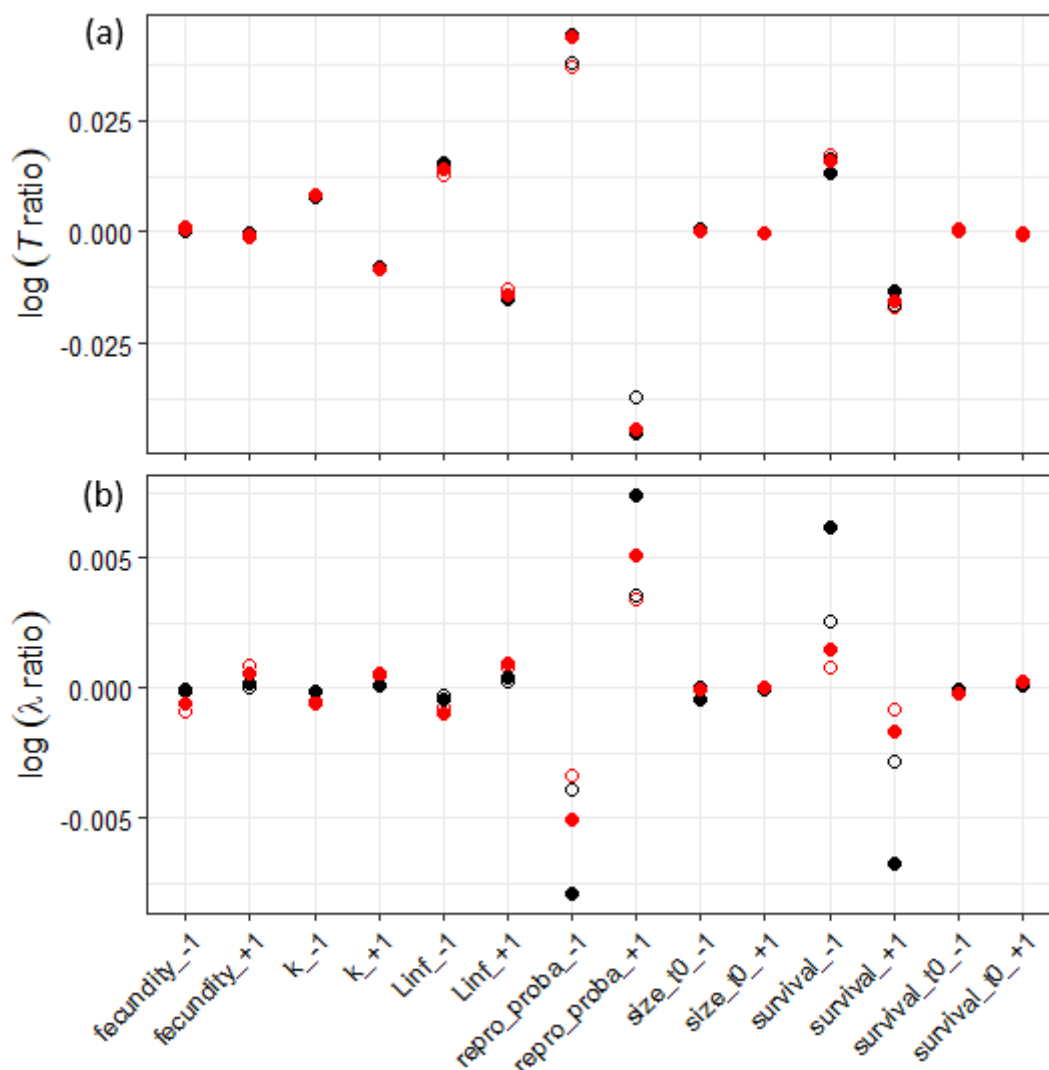
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Table S 1: Responses in size at maturity and adult size to warming and food increase in the experimental studies. The symbols +, - and x indicate a positive, negative or no effect of the variable, respectively.

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.



835

836 **Fig. S 5: Sensitivity analysis of (a) generation time T and (b) asymptotic per capita population growth rate λ .**837 Black and red colors correspond to the cold and warm treatments, respectively. Filled and empty circles correspond to the
838 median of ad libitum and food restriction treatments, respectively.

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

848 Demographic parameters are most sensitive to variability in reproductive probability (Fig. S 5).
849 Since we consider all fish to reproduce with probability = 1 from sexual maturity, adding or subtracting
850 1 % to the slope of the regression is equivalent to increasing or decreasing age at sexual maturity by
851 13.7, 10.3, 2.4, and 1.8 days for conditions ad_20, res_20, ad_30, and res_30, respectively. Not
852 surprisingly, this input strongly influences the demographic parameters since in the model the length
853 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 Bertalanfy 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.