



**HAL**  
open science

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

Simon Bazin, Claire Hemmer-Brepson, Maxime Logez, Arnaud Sentis, Martin Daufresne

## ► To cite this version:

Simon Bazin, Claire Hemmer-Brepson, Maxime Logez, Arnaud Sentis, Martin Daufresne. Distinct impacts of food restriction and warming on life history traits affect population fitness in vertebrate ectotherms. 2023. hal-03738584v3

**HAL Id: hal-03738584**

**<https://hal.inrae.fr/hal-03738584v3>**

Preprint submitted on 9 May 2023 (v3), last revised 9 May 2023 (v4)

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

# 1 Distinct impacts of food restriction and warming 2 on life history traits affect population fitness in 3 vertebrate ectotherms

4

5 **Simon BAZIN<sup>1, 2, \*</sup>, Claire HEMMER-BREPSON<sup>2</sup>, Maxime LOGEZ<sup>2, 3</sup>, Arnaud SENTIS<sup>2, #</sup> and Martin**  
6 **DAUFRESNE<sup>2, #</sup>**

7 <sup>1</sup>Univ. Savoie Mont Blanc, INRAE, CARRTEL, 74200 Thonon-les-Bains, France

8 <sup>2</sup>INRAE, Aix Marseille Univ., RECOVER, Aix-en-Provence, France

9 <sup>3</sup>INRAE, RIVERLY, F-69625, Villeurbanne Cedex, France

10 Corresponding author: [simon.bazin@inrae.fr](mailto:simon.bazin@inrae.fr)

11 # These authors contributed equally to this work

12

## 13 Abstract

14

15 The reduction of body size with warming has been proposed as the third universal response to  
16 global warming, besides geographical and phenological shifts. Observed body size shifts in ectotherms  
17 are mostly attributed to the temperature size rule (TSR) stating that warming speeds up initial growth  
18 rate but leads to smaller size when food availability does not limit growth. Nevertheless, climate  
19 warming can decrease food availability by modifying biochemical cycles and primary production. Food  
20 availability can also influence growth, fecundity and survival and thus potentially modulate the effect  
21 of temperature on life history strategies and fitness. However, the interactive effects of temperature  
22 and food availability on life history traits have been mostly studied in small invertebrate species where  
23 life history traits have been mainly considered in isolation. In contrast, we have limited information on  
24 (1) how temperature and food availability jointly influence life history traits in vertebrate predators  
25 and (2) how changes in different life history traits combines to influence fitness and population growth.  
26 To fill this gap, we investigated under laboratory conditions the independent and interactive effects of  
27 temperature (20 or 30 °C) and food availability (restricted or *ad libitum*) on the growth, fecundity and  
28 survival of the medaka fish *Oryzias latipes*. We next used our empirical estimates of vital rates as input  
29 parameters of an Integral Projection model (IPM) to predict how modifications in vital rates translate  
30 into generation time and population growth rate (i.e. mean fitness). Our results confirm that warming  
31 leads to a higher initial growth rate and lower size leading to crossed growth curves between the two  
32 temperatures. Food-restricted fish were smaller than *ad libitum* fed fish throughout the experiment,  
33 leading to nested growth curves. Fish reared at 30 °C matured younger, had smaller size at maturity,  
34 had a higher fecundity but had a shorter life span than fish reared at 20 °C. Food restriction increased  
35 survival probabilities under both temperature conditions corresponding to a "eat little die old"  
36 strategy. According to the IPM, warming reduces generation time and increases mean fitness in  
37 comparison to the cold treatments. Food restriction increased generation time and fitness in the cold  
38 treatment but had no effect in the warm treatment. Our results highlight the importance of accounting  
39 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.

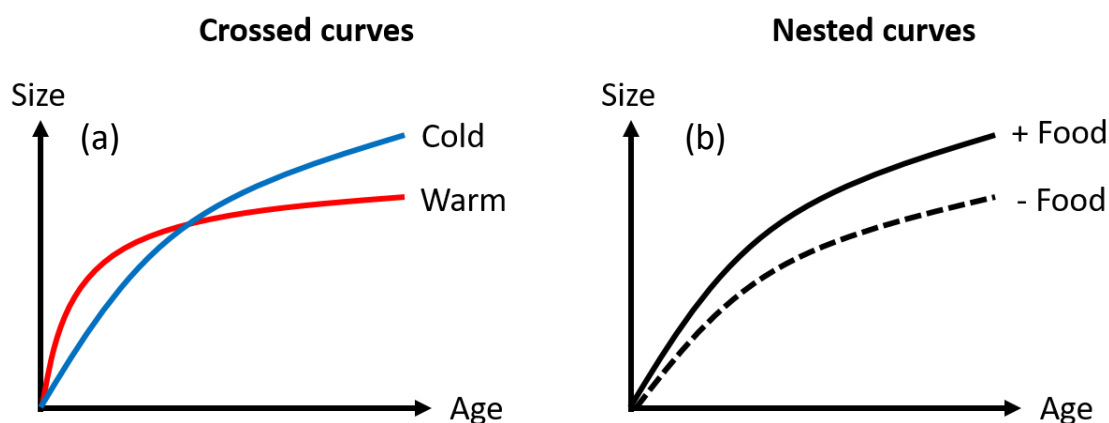
82 Besides temperature, another major factor underlying growth, reproduction and survival is  
83 food availability (Boggs and Ross 1993, Giberson and Rosenberg 1992, Boersma and Vijverberg 1996,  
84 Corrêa *et al.* 2021). Individuals need enough resources, as energy and material inputs, to sustain 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 Ostefeld 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<sup>-1</sup>). 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 F<sub>0</sub> 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 F<sub>0</sub> 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 F<sub>1</sub> 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<sup>®</sup> (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<sup>®</sup> 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  $t$ ,  $L_\infty$  the maximum asymptotic size (i.e. the total length  
208 for fish with an  $\infty$  age),  $K$  the initial growth rate, and  $t_0$  the theoretical age at which body size is null.

209 Von Bertalanffy growth curves parameters ( $L_\infty$ ,  $K$ ,  $t_0$ ) 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  $L_\infty$ , 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  $L_\infty$ ,  $K$  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  $\varepsilon$  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  $\sigma_{L_\infty}$ ,  $\sigma_K$ ,  $\sigma_{t_0}$  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  $\Sigma$ , 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  $L_\infty$  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 ( $L_{\infty CT}$ ,  $K_{CT}$ ,  $t_{OCT}$ ) 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  $\lambda$ . We quantified the uncertainty of  $T$  and  $\lambda$  by bootstrapping 1000  
 305 combinations of  $L_\infty$ ,  $K$  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  $\lambda$ . This yielded 1000 estimates of  $T$  and  $\lambda$  for each experimental treatments. We next calculated  
 309 the 95 % confidence intervals of  $T$  and  $\lambda$  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  $\lambda$  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.

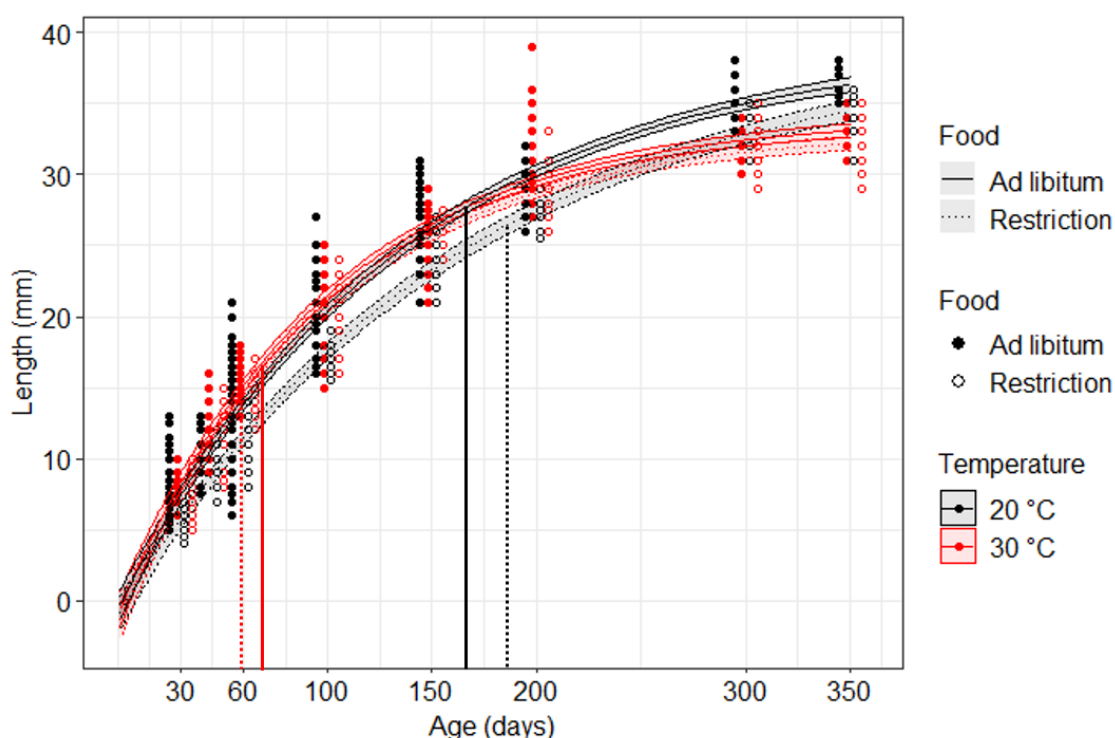
313

## 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



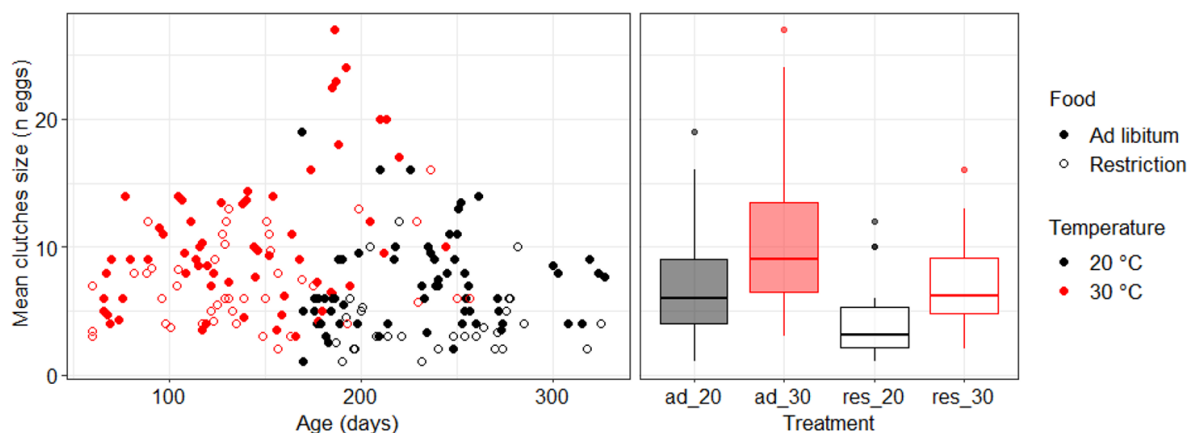
325

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).

331

332 In the warm treatment, the fish were sexually mature at  $67.3 \pm 2.3$  days (body length:  $16.8 \pm$   
 333  $0.1$  mm) under *ad libitum* condition and at 60 days for all replicates (body length:  $17.2 \pm 0.7$  mm) under  
 334 food restriction. In the cold treatment, they were sexually mature at  $169.7 \pm 0.6$  days (body length:  
 335  $26.3 \pm 0.6$  mm) and  $186.5 \pm 0.7$  days (body length:  $25.7 \pm 0.4$  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 ( $df = 1$ ,  $chi^2 = 0.79$ ,  $p = 0.37$ ).



340

341

342

343

**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.

344

345

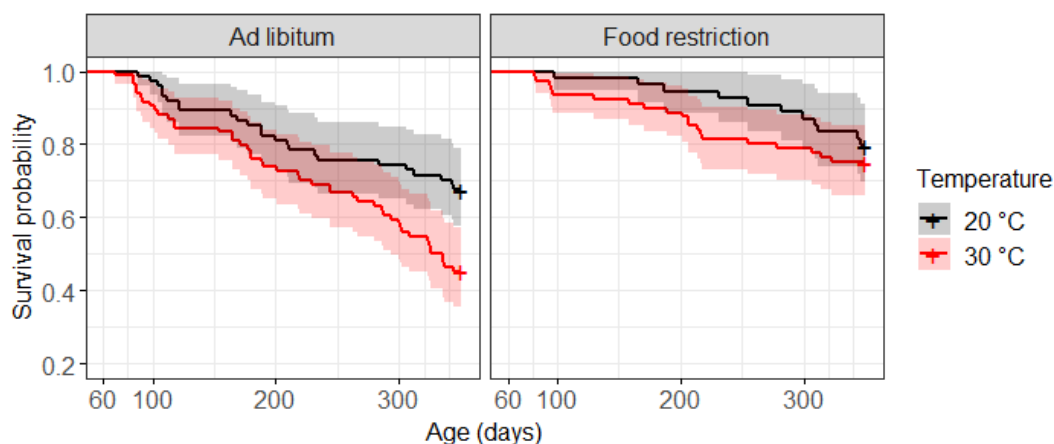
346

347

348

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**).

349



350

351

352

353

354

**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 % confidence intervals.

355

356

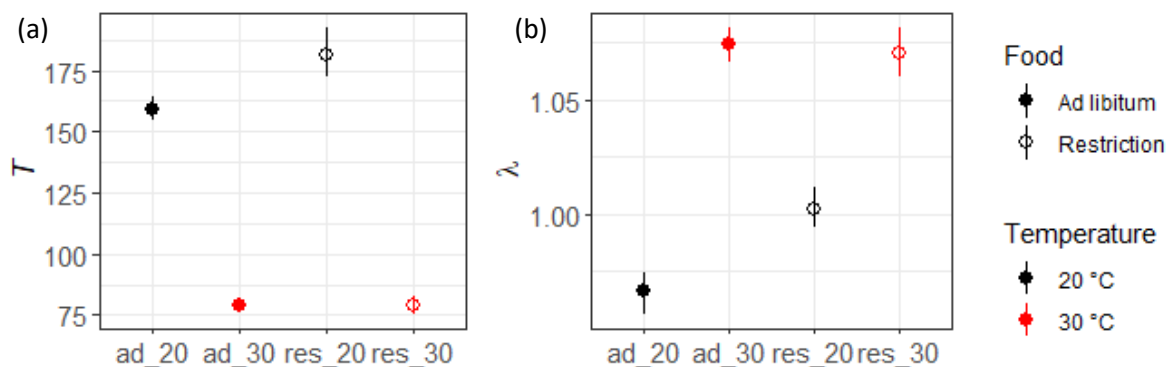
357

358

359

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

360



361

362 **Figure 5: Estimated (a) generation time  $T$  and (b) asymptotic per capita population growth rate  $\lambda$  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.

## 496 Acknowledgements

497 We thank the technical team and all people involved in the laboratory experiment for their help with  
 498 fish rearing. We thank the recommender Aleksandra Walczyńska and the reviewers Wolf Blanckenhorn  
 499 and Wilco Verberk for their insightful comments that helped to improve the manuscript quality.

## 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  
 504 this article.

## 505 Funding

506 This work was supported by the ANR project EcoTeBo (ANR-19-CE02-0001-01) from the French  
 507 National Research Agency (ANR) to A. S.

## 508 References

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

- 603 Forster, Jack, Andrew G. Hirst, and David Atkinson. 2012. "Warming-Induced Reductions in Body Size  
604 Are Greater in Aquatic than Terrestrial Species." *Proceedings of the National Academy of Sciences*  
605 109 (47): 19310–14. <https://doi.org/10.1073/pnas.1210460109>.
- 606 Frazier, Melanie R., H. Arthur Woods, and Jon F. Harrison. 2001. "Interactive Effects of Rearing Tem-  
607 perature and Oxygen on the Development of *Drosophila Melanogaster*." *Physiological and Biochemi-  
608 cal Zoology* 74 (5): 641–50. <https://doi.org/10.1086/322172>.
- 609 Fryxell, David C., Alexander N. Hoover, Daniel A. Alvarez, Finn J. Arnesen, Javiera N. Benavente,  
610 Emma R. Moffett, Michael T. Kinnison, Kevin S. Simon, and Eric P. Palkovacs. 2020. "Recent Warming  
611 Reduces the Reproductive Advantage of Large Size and Contributes to Evolutionary Downsizing in Na-  
612 ture." *Proceedings. Biological Sciences* 287 (1928): 20200608.  
613 <https://doi.org/10.1098/rspb.2020.0608>.
- 614 Gardner, Janet L., Anne Peters, Michael R. Kearney, Leo Joseph, and Robert Heinsohn. 2011. "Declin-  
615 ing Body Size: A Third Universal Response to Warming?" *Trends in Ecology & Evolution* 26 (6): 285–  
616 91. <https://doi.org/10.1016/j.tree.2011.03.005>.
- 617 Giberson, Donna J., and David M. Rosenberg. 1992. "Effects of Temperature, Food Quantity, and  
618 Nymphal Rearing Density on Life-History Traits of a Northern Population of *Hexagenia* (Ephemero-  
619 ptera:Ephemeridae)." *Journal of the North American Benthological Society* 11 (2): 181–93.  
620 <https://doi.org/10.2307/1467384>.
- 621 Gibert, Jean P., and John P. DeLong. 2014. "Temperature Alters Food Web Body-Size Structure." *Biol-  
622 ogy Letters* 10 (8): 20140473. <https://doi.org/10.1098/rsbl.2014.0473>.
- 623 Giebelhausen, B., and W. Lampert. 2001. "Temperature Reaction Norms of *Daphnia Magna*: The Ef-  
624 fect of Food Concentration." *Freshwater Biology* 46 (3): 281–89. [https://doi.org/10.1046/j.1365-  
625 2427.2001.00630.x](https://doi.org/10.1046/j.1365-2427.2001.00630.x).
- 626 Gredilla, Ricardo, Alberto Sanz, Monica Lopez-Torres, and Gustavo Barja. 2001. "Caloric Restriction  
627 Decreases Mitochondrial Free Radical Generation at Complex I and Lowers Oxidative Damage to Mi-  
628 tochondrial DNA in the Rat Heart." *The FASEB Journal* 15 (9): 1589–91. [https://doi.org/10.1096/fj.00-  
629 0764fje](https://doi.org/10.1096/fj.00-0764fje).
- 630 Hemmer-Brepson, C., L. Replumaz, C. Romestaing, Y. Voituron, and M. Daufresne. 2014. "Non-Stress-  
631 ful 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>.
- 633 Hirshfield, Michael F. 1980. "An Experimental Analysis of Reproductive Effort and Cost in the Japa-  
634 nese Medaka, *Oryzias Latipes*." *Ecology* 61 (2): 282–92. <https://doi.org/10.2307/1935187>.
- 635 Hoefnagel, K. Natan, and Wilco C. E. P. Verberk. 2015. "Is the Temperature-Size Rule Mediated by Ox-  
636 ygen in Aquatic Ectotherms?" *Journal of Thermal Biology, What sets the limit? How thermal limits,  
637 performance and preference in ectotherms are influenced by water or energy balance*, 54 (Decem-  
638 ber): 56–65. <https://doi.org/10.1016/j.jtherbio.2014.12.003>.
- 639 Horne, Curtis R., Andrew. G. Hirst, and David Atkinson. 2015. "Temperature-Size Responses Match  
640 Latitudinal-Size Clines in Arthropods, Revealing Critical Differences between Aquatic and Terrestrial  
641 Species." *Ecology Letters* 18 (4): 327–35. <https://doi.org/10.1111/ele.12413>.
- 642 Johnston, Ian A, Sujatha Manthri, Richard Alderson, Patrick Campbell, David Mitchell, David Whyte,  
643 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. Burkepille. 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>.

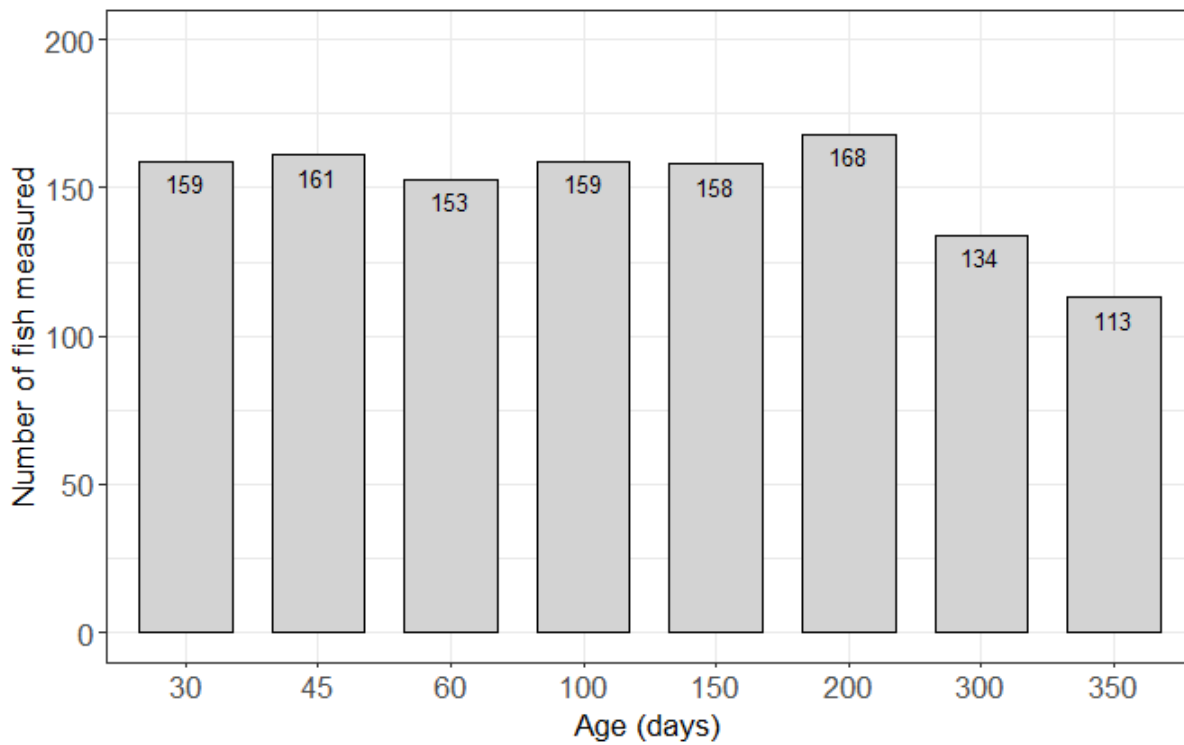
- 684 Paerl, Hans, and Jef Huisman. 2008. "Blooms Like It Hot." *Science (New York, N.Y.)* 320 (May): 57–58.  
685 <https://doi.org/10.1126/science.1155398>.
- 686 Paerl, Hans W. 2014. "Mitigating Harmful Cyanobacterial Blooms in a Human- and Climatically-Im-  
687 pacted World." *Life* 4 (4): 988–1012. <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 Wojewodzic, 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 Sipel. 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>.

797 Appendix

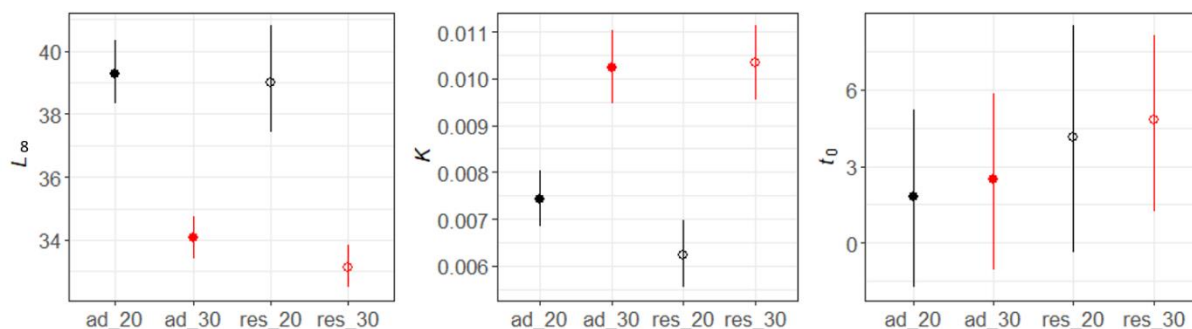
798



799

800

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



801

802

803

804

**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.

805

806

807

808

809

810

811

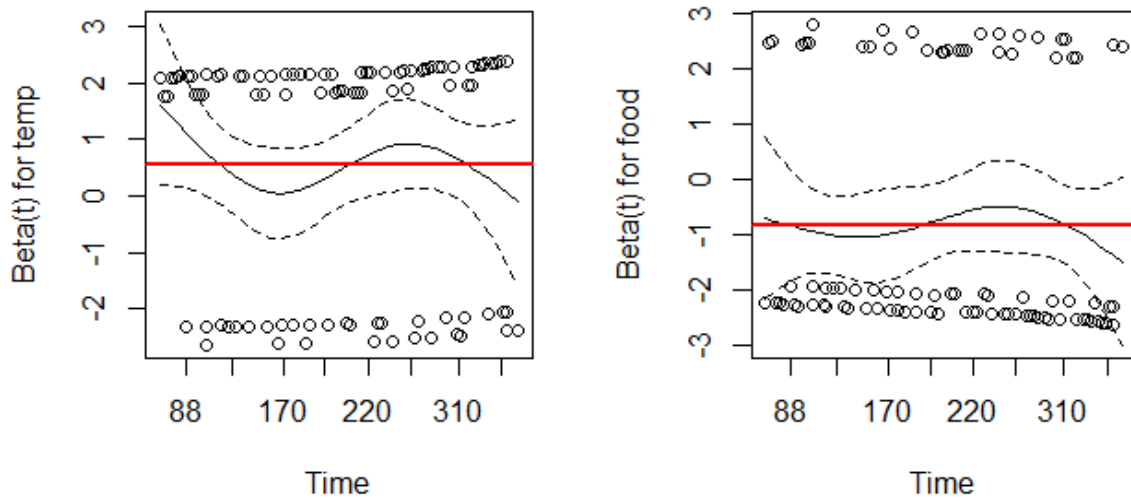
812

813

814

Consistent with the experimental curves and TSR, warming significantly increased the initial growth rate  $K$  and decreased the maximum asymptotic size  $L_{\infty}$ . 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  $L_{\infty}$ , 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.





815

816

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

817

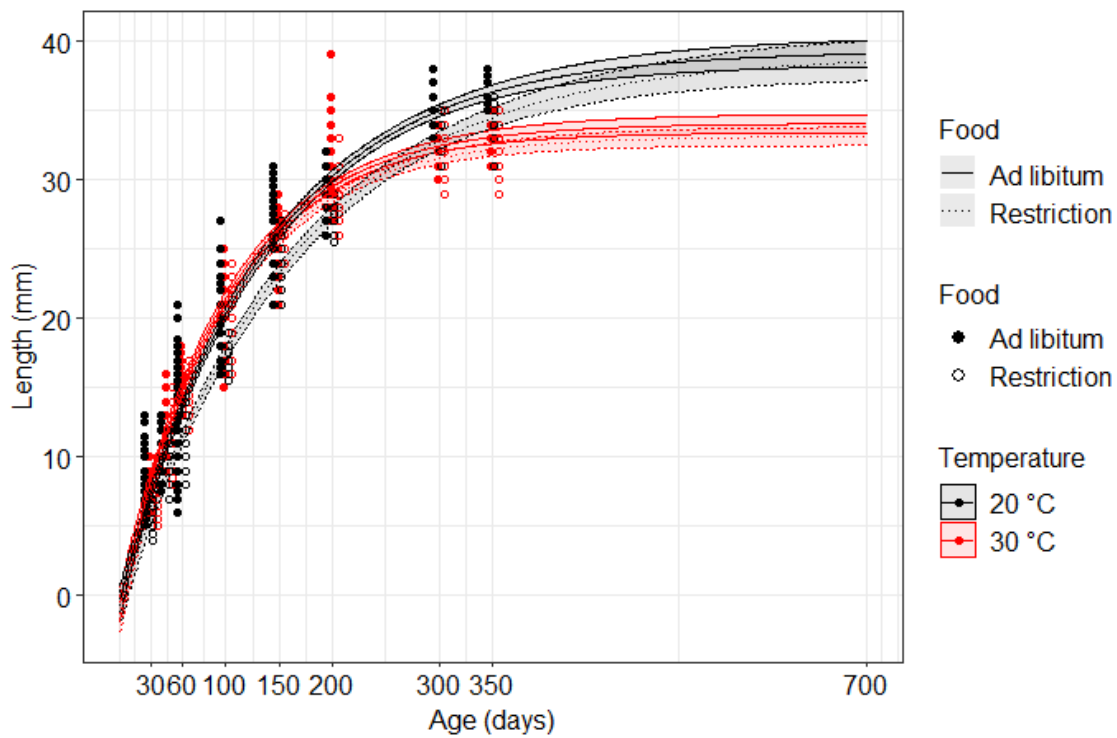
818

819

820

821

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.



822

823

824

825

826

827

**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.

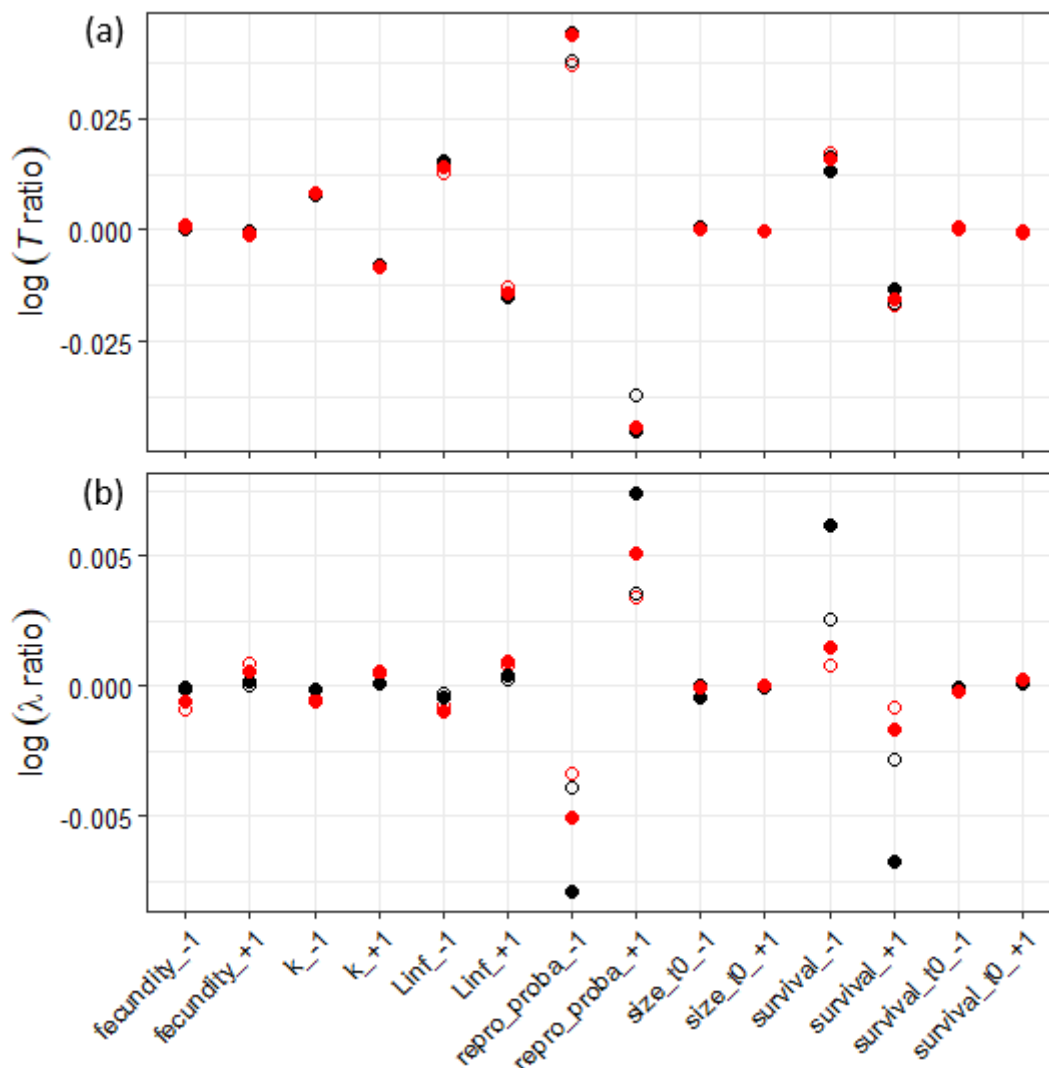
828  
829

**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
<b>Betini <i>et al.</i> (2020)</b>	Warming	x	-
	Food	x	+
<b>Courtney-Jones <i>et al.</i> (2015)</b>	Warming	-	
	Food	-	
<b>Giberson and Rosenberg (1992)</b>	Warming		+
	Food		+
<b>Giebelhausen and Lampert (2001)</b>	Warming	-	
	Food	-	
<b>Kielbasa <i>et al.</i> (2014)</b>	Warming		
	Food		
	Interaction		Adult size reduction with only 1 of 2 nutritional qualities
<b>Lee and Roh (2010)</b>	Warming		
	Food		
	Interaction	Mass at pupation reduction under extreme food conditions	
<b>Marn <i>et al.</i> (2017)</b>	Warming	x	x
	Food	x	+
<b>McLeod <i>et al.</i> (2013)</b>	Warming	x	
	Food	x	
<b>Rohner <i>et al.</i> (2017)</b>	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  $\lambda$ .**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  $\lambda$  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  $L_{\infty}$  by adding or  
844 subtracting 1% to their mean values. We then investigated the sensitivity of  $T$  and  $\lambda$  by calculating the  
845 log ratio of the parameter ( $\lambda$  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  $L_{\infty}$  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.