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Distinct impacts of food restriction and warming on growth, reproduction and survival

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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 adult size when food availability does not limit growth. Nevertheless, climate warming can decrease food availability by modifying biochemical cycles and primary production. The interactive effects of temperature and food availability on life history traits have been studied in small invertebrate species, but we have limited information on how temperature and food availability jointly influence life history traits in vertebrate predators, despite the observation that TS responses are amplified in larger species. Food availability can also influence growth, fecundity and survival and thus potentially modulate the effect of temperature on life history strategies. In this paper, we filled this gap by investigating 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*. Our results confirm that warming leads to a higher initial growth rate and lower adult 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. In addition, food restriction appears to amplify TSR by decreasing initial growth rate in the cold treatment. 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, suggesting a "live fast die young" strategy under warming. Food restriction increased the survival probability under both temperature conditions corresponding to a "eat little die old" strategy. Finally, food restriction appeared to be advantageous as food restriction largely increased survival while have a weaker negative effect on growth and fecundity and no impact on age and size at maturity. Our results highlight the importance of accounting for the interaction between temperature and food availability to understand body size shifts. This is of importance in the context of global warming as resources (e.g., phytoplankton and zooplankton communities in aquatic ecosystems) are predicted to change in size structure and total abundance with increasing temperatures. Furthermore, we highlight the importance of considering ontogeny when investigating the effects of temperature-induced body size shifts on trophic interactions and community dynamics since thermal effects depend on the life stage of the organisms.

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

41 Introduction

42

43 Body size reduction has been proposed as a third universal species response to global warming
44 (Daufresne *et al.* 2009, Gardner *et al.* 2011, Sheridan and Bickford 2011), in addition to changes in
45 phenology (Visser and Both 2005) and geographic distribution (Parmesan and Yohe 2003). While the
46 first two responses have been studied extensively (Meyer *et al.* 1999), the third one has received less
47 attention despite its high prevalence and magnitude. For instance, body size can reduce up to -4 %
48 per °C in terrestrial species and up to -8 % per °C in aquatic ectotherms (Forster *et al.* 2012). Previous
49 studies focused mainly on proximal mechanisms of body size changes (Zuo *et al.* 2012, Atkinson and
50 Sibly 1997, Frazier *et al.* 2001, Hoefnagel and Verberk 2015, Verberk *et al.* 2021), i.e. how
51 environmental factors influence life history traits by impacting physiological and developmental
52 processes (Thierry 2005), and their variability among species and habitats (Horne *et al.* 2015, Forster
53 *et al.* 2012, Atkinson 1994). In aquatic systems, warming decreases oxygen concentration and hypoxia
54 tends to amplify TS responses which has been interpreted as a response to limited oxygen resource
55 (Frazier *et al.* 2001, Hoefnagel and Verberk 2015, Verberk *et al.* 2021). In contrast, the oxygen resource
56 is not limiting in terrestrial system which may explain why TS responses are weaker in terrestrial than
57 in aquatic ecosystems (Forster *et al.* 2012). At the individual level, body size shift can be explained by
58 the impact of temperature on the growth of ectotherms (Atkinson and Sibly 1997, Berrigan and
59 Charnov 1994, Perrin 1995, Arendt 2007, Arendt 2011). Following the "Temperature Size Rule" (TSR,
60 Atkinson 1994), ectotherms grow faster but reach a smaller asymptotic size under warm environment
61 compared to colder ones, resulting in "crossed" growth curves (Figure 1). In addition to proximal
62 mechanisms explaining the TSR, ultimate mechanisms relating to past conditions influencing growth,
63 development, and general life-history strategies take more of an evolutionary perspective (e.g.
64 survival) (Thierry 2005). This pattern of TSR remains an evolutionary puzzle (Atkinson and Sibly 1997)
65 and could represent different growing and/or developing strategies. For example, a recent study
66 showed that warming accelerates growth and reproduction leading to a rapid life cycle but also a
67 decrease in adult survival in a temperate lizard species, a strategy commonly referred to as "live fast
68 die young" (Bestion *et al.* 2015). This study and others (Stillwell *et al.* 2007, Marn *et al.* 2017, Courtney
69 Jones *et al.* 2015, Corrêa *et al.* 2021, Clissold and Simpson 2015, Kingsolver *et al.* 2006, Rohner *et al.*
70 2017) suggest that it is important to investigate the links between growth trajectories and fitness
71 related traits (survival and fecundity) to better understand trade-offs among traits and evolutionary
72 strategies. However, most studies on TSR did not investigate covariations between growth and other
73 phenotypic traits (but see Stillwell *et al.* 2007, Marn *et al.* 2017, Corrêa *et al.* 2021, Kingsolver *et al.*
74 2006) which limits our ability to detect situations in which TSR might be adaptive (i.e. increase fitness)
75 or maladaptive.

76 Besides temperature, another major factor underlying growth, reproduction and survival is
77 food availability (Boggs and Ross 1993, Giberson and Rosenberg 1992, Boersma and Vijverberg 1996,
78 Corrêa *et al.* 2021). Individuals need enough resources, as energy and material inputs, to sustain their
79 metabolic demand and optimize the allocation of energy to growth, reproduction and maintenance
80 (Lemoine and Burkepille 2012, Brown *et al.* 2004, Cross *et al.* 2015). There is a long history of researches
81 on the influence of food availability on the growth rate and fecundity of ectothermic species
82 (Rasmussen and Ostfeld 2000, Johnston *et al.* 2002, Giberson and Rosenberg 1992, Boersma and
83 Vijverberg 1996, Corrêa *et al.* 2021). In most cases, individuals with a higher food availability have a
84 higher fecundity and have both a higher initial growth rate and a larger asymptotic size compared to

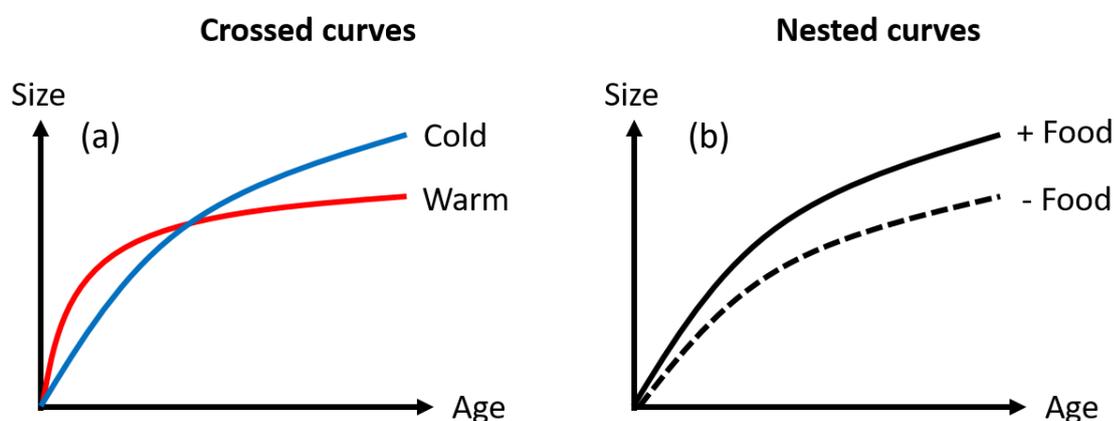
85 individuals under food restriction. In contrast to the pattern of crossed curves driven by temperature,
86 different resource levels lead to a pattern of nested curves where the growth curve under limiting
87 resources is nested below the growth curve under unlimited resources (Figure 1). Interestingly, food
88 restriction may also be beneficial to the lifespan of organisms as this restriction reduces the production
89 of senescence-accelerating oxidizing agents during metabolism (Sohal and Weindruch 1996, Gredilla
90 *et al.* 2001, Speakman 2005), resulting in a “eat little die old” strategy. The effects of food restriction
91 on fecundity (which decreases) and survival probability (which increases) are thus opposite and can be
92 explained by a resources distribution to nutrient-limited processes (Corrêa *et al.* 2021).

93 Phenological and geographical changes can alter the quantity and quality of resources in
94 predator-prey relationships by inducing temporal or spatial mismatches where the predator is left with
95 reduced food availability (Boukal *et al.* 2019, Twining *et al.* 2022). For instance, a temporal shift in the
96 spring bloom of diatoms explained the long-term decline of a daphnia population in a large temperate
97 lake because of a temporal mismatch between the diatom bloom and the beginning of the growing
98 season for the daphnia population (Winder and Schindler 2004). Along the same line, Visser *et al.*
99 (2006) showed that asynchrony between caterpillar biomass and the offspring feeding requirements
100 of an insectivorous bird affected the number and weight of fledged birds. These phenological
101 asynchronies can alter the structure and dynamics of food webs and modify ecosystem processes
102 (Damien and Tougeron 2019, Renner and Zohner 2018). Moreover, warming can also decrease food
103 quality by benefiting small phytoplankton taxa of low nutritional quality such as picocyanobacteria or
104 filamentous bacteria (Paerl and Huisman 2008, Paerl 2014, Ekvall *et al.* 2013, Urrutia-Cordero *et al.*
105 2017). Altogether, these studies indicate that it is important to investigate the direct effects of
106 temperature as well as indirect effects such as altered food quality and availability to better
107 understand the impact of climate change on growth, survival and fecundity.

108 The interactive effects of temperature and food availability on life history traits have been
109 studied in invertebrates such as daphnia (Betini *et al.* 2020, Giebelhausen and Lampert 2001,
110 Wojewodzic *et al.* 2011, Persson *et al.* 2011), aquatic insect larvae (Giberson and Rosenberg 1992) and
111 terrestrial insects (Clissold and Simpson 2015, Corrêa *et al.* 2021, Stillwell *et al.* 2007, Kingsolver *et al.*
112 2006, Rohner *et al.* 2017). In these studies, warming generally resulted in a rapid life cycle by increasing
113 growth rates and decreasing age and size at maturity as well as survival. However, these thermal
114 effects were often modulated by food availability. For example, Betini *et al.* (2020) found body size
115 reduction under warming was five time stronger under limited food availability compared to unlimited
116 conditions. Moreover, temperature and food availability can covary and impact ectotherm life history
117 traits. Koussoroplis and Wacker (2016) showed that the effect of food restriction on life history traits
118 is more severe when temperature moves away from the optimal temperature. Nevertheless, all the
119 studies mentioned above were conducted on small invertebrate species. As a result, we have no
120 information on how temperature and food availability jointly influence life history traits of vertebrate
121 predators, despite the observation that TS responses are amplified in larger species (Forster *et al.*
122 2012). This is because of importance as body size changes in predatory species can alter the trophic
123 interaction strength and food webs stability (Emmerson and Raffaelli 2004, Sentis *et al.* 2017, Osmond
124 *et al.* 2017). We must therefore consider both the direct physiological impact of temperature as well
125 as its indirect effects through modified food availability on body size changes and life history traits of
126 predatory species to better understand and predict the consequences of climate change across trophic
127 levels.

128 In this study, we address this gap by experimentally investigating growth, reproduction and
 129 survival of a vertebrate predatory species, the medaka fish (*Oryzias latipes*, Temminck & Schlegel),
 130 raised at two temperatures (20 and 30 °C) with and without food restriction. Our objective was to test
 131 whether TSR was maintained under food-restricted conditions and whether food restriction
 132 modulated the effects of temperature on the developmental strategies, fecundity and survival of a
 133 vertebrate predatory species. We expected warming to result in a rapid life style with faster growth
 134 but lower survival but these thermal effects would be modulated by food restriction, which increases
 135 survival and selects for late maturation at larger body size. We discuss the implication of our findings
 136 on (i) the importance of accounting for the temperature-food interaction in the context of global
 137 warming, as we expect the quantity and quality of resources to change and (ii) to which extent
 138 investigating growth, reproduction and survival patterns could help disentangling the relative impacts
 139 of temperature and resources availability on body size shifts under global warming.

140



141

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

144

145 Material and methods

146 Biological system and rearing conditions

147

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

156 The parental F₀ generation consisted in a total of 76 fish (approximately 120 days old) of the
 157 CAB strain provided by Carolina Biological Supply Company (Burlington, NC, USA ; from AMAGEN, Gif-
 158 sur-Yvette, France) and WatchFrog (Evry, France). At reception, fish were kept for 5 days at 25 °C. Then,

159 half of the fish were placed into five 20 L tanks for the "cold" thermal regime and the other half were
 160 placed into five 20 L tanks for the "warm" thermal regime. The female to male sex ratio per tank ranged
 161 from 1.33 to 1.66. The tank temperatures were increased or decreased by 0.5 °C every days until they
 162 reached 30 °C or 20 °C. During this acclimation period, the photoperiod was 12h: 12h (day: night) and,
 163 after acclimation, it was then adjusted to 16h: 8h (day: night) which is optimal for medaka reproduction
 164 (Hirshfield 1980).

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

179

180 Growth, fecundity and survival

181

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

191 Statistical analysis

192

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

$$195 \quad L_t = L_\infty (1 - e^{-k(t-t_0)}) \text{ (eq. 1)}$$

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

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

$$206 \quad L_{\infty CT} \sim N(0, 0.001) \quad K_{CT} \sim N(0, 0.001) \quad t_{0CT} \sim N(0, 0.001) \quad (\text{eq. 2})$$

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

$$209 \quad \begin{vmatrix} \sigma_{L_\infty}^2 & r_1 \cdot \sigma_{L_\infty} \cdot \sigma_K & r_2 \cdot \sigma_{L_\infty} \cdot \sigma_{t_0} \\ r_1 \cdot \sigma_{L_\infty} \cdot \sigma_K & \sigma_K^2 & r_3 \cdot \sigma_K \cdot \sigma_{t_0} \\ r_2 \cdot \sigma_{L_\infty} \cdot \sigma_{t_0} & r_3 \cdot \sigma_K \cdot \sigma_{t_0} & \sigma_{t_0}^2 \end{vmatrix} \quad (\text{eq. 3})$$

210 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
 211 correlations between these vectors. We used uninformative priors with a uniform distribution for each
 212 parameter of Σ , adapting the limits to the parameters (e.g between -1 and 1 for a correlation).

213 $L_{\infty CT}$, K_{CT} and t_{0CT} are thus hyperpriors (population parameters) that serve to assess parameters for
 214 each tank (t) when associated with the random effects. For instance for the L_∞ parameter:

$$215 \quad L_{\infty t} = L_{\infty CT} + \varepsilon_{L_{\infty t}} \quad (\text{eq. 4})$$

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

$$218 \quad L_{tj} = L_{\infty t} \left(1 - e^{-k_t(t_j - t_{0t})} \right) \quad (\text{eq. 5})$$

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

$$220 \quad \begin{matrix} L_{ftj} \sim N(L_{tj}, \sigma) \\ \sigma \sim U(0, 10) \end{matrix} \quad (\text{eq. 6})$$

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

232 We investigated the effects of temperature, food restriction and their interaction (fixed ef-
 233 fects) on mean daily clutch size per female (log transformed) and survival probability using a linear

234 mixed effects model (*lmer* function in the “lme4” package (Bates *et al.* 2015)) and a mixed effects Cox
 235 proportional hazards model (*coxme* function in the “coxme” package (Therneau *et al.* 2022)), respec-
 236 tively, with tank as random factor. For both models, analyses of deviance using Wald tests were pro-
 237 vided to test the significance of fixed parameters. We tested the assumptions of the mixed effects Cox
 238 proportional hazards model using the *cox.zph* function (“survival” package (Therneau *et al.* 2022))
 239 which correlates the corresponding set of scaled Schoenfeld residuals with time to test for
 240 independence between residuals and time (see Fig. S 3 for more details).

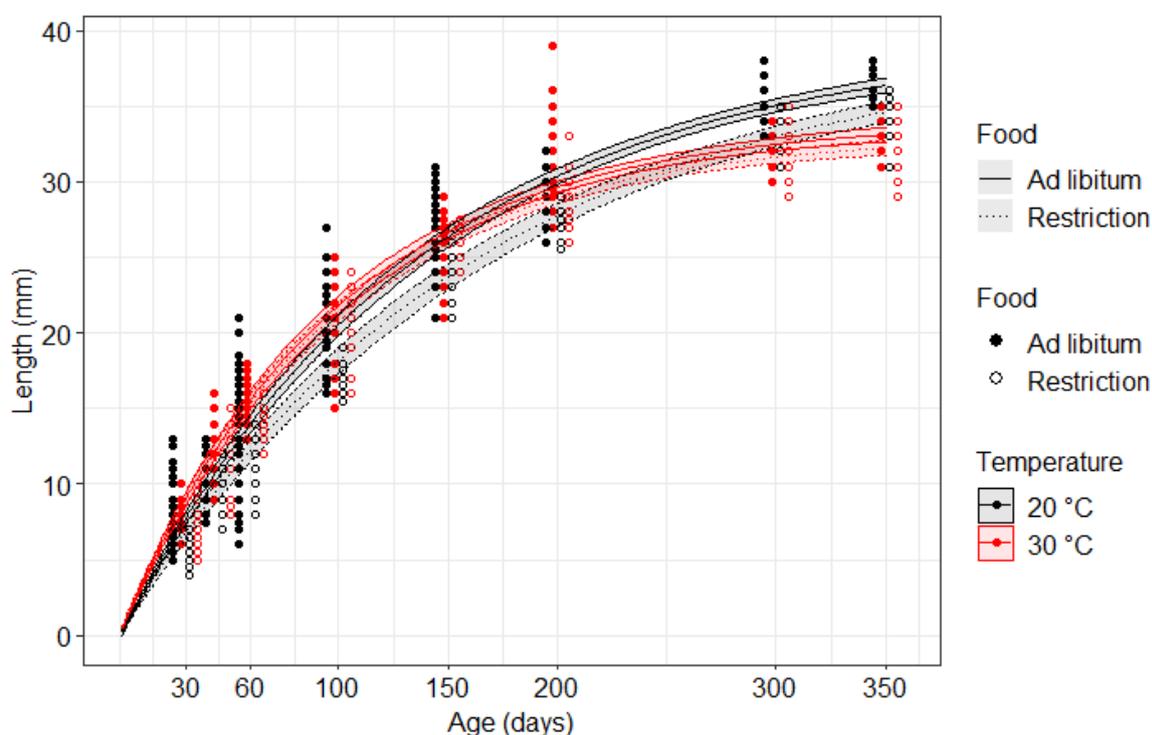
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242 Results

243

244 We found that, at both food conditions, warming leads to crossed growth curves by increasing
 245 initial growth rate and decreasing adult size, although the curves crossed later for the food-restricted
 246 fish (Figure 2). Food restriction in the cold treatment leads to nested growth curves throughout the
 247 experiment by decreasing the initial growth rate and adult size. Growth curves also tended to be
 248 nested in the warm treatment although the credibility intervals overlapped until day 220 and the
 249 curves were only significantly different toward the end of the experiment (from day 220 to day 300,
 250 Figure 2).

251



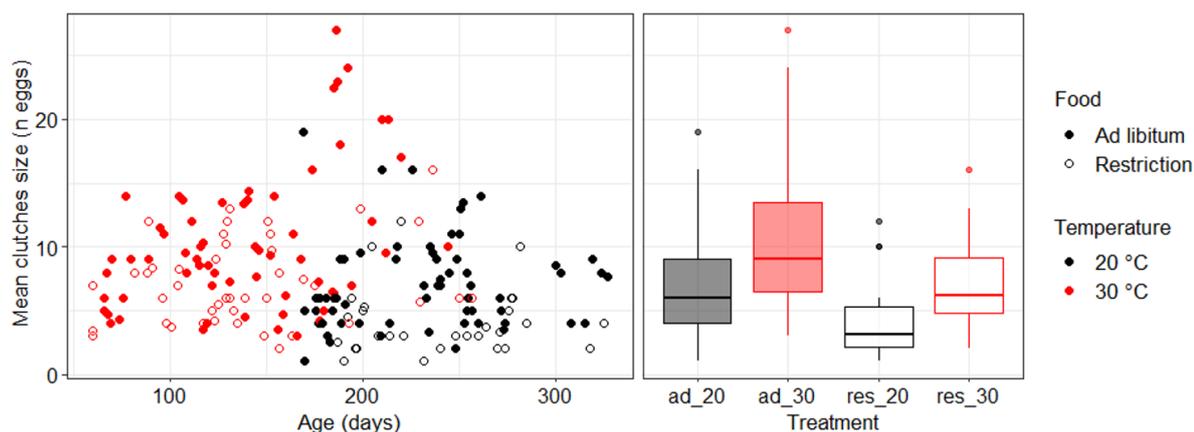
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253 **Figure 2: Fitted von Bertalanffy growth curve for each combination of temperature and food conditions.**

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

258 In the warm treatment, the fish were sexually mature at 67.3 ± 2.3 days (body length: $16.8 \pm$
 259 0.1 mm) under *ad libitum* condition and at 60 days for all replicates (body length: 17.2 ± 0.7 mm) under
 260 food restriction. In the cold treatment, they were sexually mature at 169.7 ± 0.6 days (body length:
 261 26.3 ± 0.6 mm) and 186.5 ± 0.7 days (body length: 25.7 ± 0.4 mm) under *ad libitum* and food restriction
 262 conditions, respectively (Figure 3). We found that warming increased mean daily clutch size per female
 263 ($df = 1$, $Chi^2 = 13.26$, $p < 0.001$) and food restriction decreased it ($df = 1$, $Chi^2 = 10.58$,
 264 $p = 0.001$). Mean daily clutch size per female was not dependent on the interaction between
 265 temperature and food conditions ($df = 1$, $chi^2 = 0.79$, $p = 0.37$).

266



267

268 **Figure 3: Temperature and food restriction effects on mean daily clutch size per female.**

269 Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively.

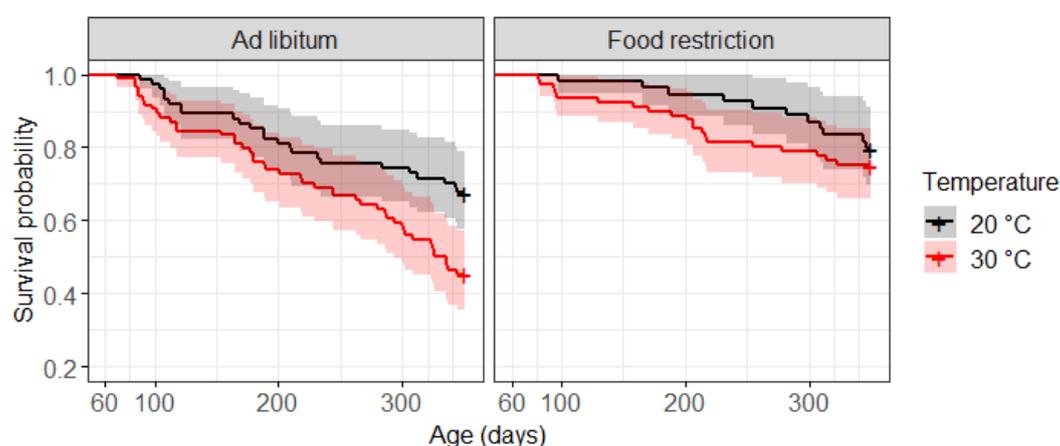
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270 Filled and empty points and boxplot represent the *ad libitum* and food restriction treatments, respectively.

271

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

276



277

278 **Figure 4: Kaplan-Meier survival curves for each combination of temperature and food conditions.**

279 Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively. Solid and dashed lines
 280 represent the *ad libitum* and the food restriction treatments, respectively. Shaded areas around the lines represent the 95 %
 281 confident intervals.

282 Discussion

283

284 Body size is a key trait in ecology as it affects many biological and ecological properties ranging
285 from the individual to the ecosystem. Body size influences metabolism, fecundity, trophic position,
286 locomotion, trophic interactions, or food web persistence and stability (Peters 1986, Calder 1996,
287 Brown *et al.* 2004, Gibert and DeLong, 2014, Sentis *et al.* 2017, Emmerson and Raffaelli 2004, Osmond
288 *et al.* 2017, Lindmark *et al.* 2018). Shrinking body size with increasing temperature has been proposed
289 as a third universal response to global warming (Daufresne *et al.* 2009, Gardner *et al.* 2011). In addition,
290 the quantity and quality of resources are expected to change with global warming (De Senerpont
291 Domis *et al.* 2014), in response to changes in physicochemical, phenological (Visser and Both, 2005)
292 and geographical parameters (Parmesan and Yohe, 2003). The independent and interactive effects of
293 temperature and food availability on life history traits have been mainly studied in small aquatic (Betini
294 *et al.* 2020, Giebelhausen and Lampert 2001, Wojewodzic *et al.* 2011, Persson *et al.* 2011, Giberson
295 and Rosenberg 1992) and terrestrial (Clissold and Simpson 2015, Corrêa *et al.* 2021, Stillwell *et al.* 2007,
296 Rohner *et al.* 2017) invertebrate species. However, we have no information on how temperature and
297 food availability jointly influence life history traits in vertebrate predators, despite the observation that
298 TS responses are amplified in larger species (Forster *et al.* 2012) and that body size reduction at higher
299 trophic level can increase food web persistence at high temperature (Sentis *et al.* 2017). Our objective
300 was thus to test whether food availability can modulate the effects of temperature on size at age and
301 life history traits of a vertebrate predator species, the medaka fish.

302 The results of our laboratory experiment indicate that, in agreement with the TSR rule
303 (Atkinson and Sibly 1997, Berrigan and Charnov 1994, Arendt 2011), warming leads to crossed growth
304 curves with individuals growing faster but reaching a smaller adult size compared to the cold condition.
305 The ecological consequences of temperature-induced changes in body size are multiple. This would
306 result in changes in the predator-prey size ratio and because body size potentially determines prey
307 size, this has important implications for predator-prey and community dynamics (Sentis *et al.* 2017,
308 Yodzis and Innes 1992, Kalinkat *et al.* 2013, Vagnon *et al.* 2021). On a larger scale, the structuring
309 effects of body size in food webs have been widely demonstrated (Williams and Martinez 2000,
310 Emmerson and Raffaelli 2004). Size interacts with temperature because temperature alters the
311 energetic demands of organisms, and thus also alters the strength of trophic interactions. For example,
312 higher temperature has been shown to increase short-term predator-prey interaction strength and
313 predator energetic efficiency (Sentis *et al.* 2012). These different studies illustrate the importance of
314 considering size and temperature in studies of global warming effects. To date, studies examining the
315 consequences of temperature-induced body size shifts on trophic interactions, community dynamics,
316 and food web structure, only considered the reduction in adult size (Sentis *et al.* 2017, Osmond *et al.*
317 2017, Lindmark *et al.* 2018). However, a recent study showed that effects of mass and temperature on
318 metabolism are interacting such that the effect of temperature varies between large and small fish
319 (Rubalcaba *et al.* 2020), suggesting that the impacts of temperature-induced body size shifts on
320 ecosystem functioning certainly depends on life stages. Lindmark *et al.* (2022) investigated the effects
321 of temperature on individual growth rates and size structure in a food web context and suggest that
322 both direct metabolic effects and indirect effects of temperature via basal resources need to be
323 considered to understand how global warming affects community size structure.

324 Furthermore, size and temperature alter the metabolism and energy requirements of
325 organisms (Brown *et al.* 2004) which implies that food also plays a crucial role in the overall responses
326 of aquatic ecosystems to climate warming (Ruiz *et al.* 2020). In our study, despite the curves being
327 nested throughout the experiment in agreement with previous studies (Rasmussen and Ostenfeld
328 2000, Johnston *et al.* 2002), the food restriction effects appeared to be greater at 20 °C where the
329 curves were more nested than at 30 °C. This is surprising because we expected food restriction to have
330 more effect at 30 °C (as shown in McLeod *et al.* 2013, Wojewodzic *et al.* 2011, and Persson *et al.* 2011)
331 because warming increases metabolic rates which implies higher energy demand and feeding rate to
332 sustain high metabolic costs (Brown *et al.* 2004). For instance, Wojewodzic *et al.* (2011) and Persson
333 *et al.* (2011) reported that warming further amplifies the decrease in somatic growth rates of *Daphnia*
334 under low nutritional quality (high C:P ratio) compared to *Daphnia* under high nutritional quality (low
335 C:P ratio). These results suggest that temperature-induced body size shifts depend on the quantity but
336 also the quality of resources with lower resource quality amplifying the detrimental effect of warming
337 as reported in a recent study (Sentis *et al.* 2022). In our study, based on the full growth curves, food
338 restriction therefore appears to amplify TSR by decreasing initial growth rate in the cold treatment, as
339 suggested by Cross *et al.* (2015). Betini *et al.* (2020) also found a TSR amplification under food
340 restriction as the body size reduction under warming was five times stronger under food restricted
341 conditions than under unlimited food conditions. Recent studies have also shown that TSR tends to be
342 amplified under oxygen limitation, which can be also considered as a limiting resource (Frazier *et al.*
343 2001, Hoefnagel and Verberk 2015, Verberk *et al.* 2021). Nevertheless, TSR is not exclusively defined
344 by adult size, but is also frequently assessed by size at maturity (Hoefnagel and Verberk 2015, Walters
345 *et al.* 2006, Verberk *et al.* 2021). Focussing on size at maturity is more relevant to assess the influence
346 of food restriction on evolutionary strategies as it is a better determinant of fitness than asymptotic
347 size (Verberk *et al.* 2021). When considering size at maturity, food restriction did not appear to amplify
348 TSR in our study as, at each temperature, fish reached sexual maturity at a similar age and size. This
349 suggests that food restriction would not influence medaka's fitness via its effects on developmental
350 time and size at maturity. A recent study also indicates that organism's evolutionary responses to
351 warming can mitigate food restrictions, thereby avoiding constraints on whole-organism growth
352 (Verberk *et al.* 2021). For example, organisms can increase the surface area for resource uptake by
353 altering body shape, increasing organ surface area, or modulating feeding activity or locomotion
354 (Verberk *et al.* 2021).

355 For several species, warming leads to early maturation, smaller size, and increased fecundity
356 (Betini *et al.* 2020, Marn *et al.* 2017). Our results are in line with these studies as we found that fish
357 reared at 30 °C were sexually mature at a younger age, were smaller at maturity and produced a larger
358 mean daily clutch size per female. In contrast, less is known about the responses of developmental
359 rates and fecundity to covariation between temperature and food. Our results did not suggest any
360 effect of food restriction on age and size at maturity, in contrast to Betini *et al.* (2020) and Marn *et al.*
361 (2017), who found that increased food availability resulted in earlier maturation. However, we found
362 that food restriction decreased mean daily clutch size at both temperature conditions. Several studies
363 have also found that increased food availability increased fecundity in both aquatic (Betini *et al.* 2020,
364 Giberson and Rosenberg 1992) and terrestrial (Corrêa *et al.* 2021) organisms. This can be explained by
365 an increase in the amount of energy to be allocated to reproduction under unlimited food conditions.

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

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

382 Although food restriction decreased the mean daily clutch size and amplified TSR by decreasing
383 the initial growth rate under cold conditions, these effects were relatively weak compared to the
384 increase in survival probability. This may be explained by potential acclimation of medaka to rearing
385 temperatures or by food restriction being not severe enough. Reducing feeding events by half (1 out of
386 2 mornings) was considered restrictive although we cannot exclude compensatory mechanisms were
387 restricted fish would feed more when they have access to food. Although this remains to be
388 investigated in more details, our results highlight the importance of considering the interactions
389 between temperature, body size and food to understand how larger predatory species respond to
390 global changes in terms of developmental and life history strategies. Indeed, warming resulted in a
391 rapid life style and increased fecundity at the cost of lower survival probability. However, food
392 restriction modulated the effects of temperature and ultimately appeared to be evolutionarily
393 advantageous since its positive effects on survival were accompanied by a weak decrease in growth
394 and fecundity, and did not impact developmental times. Under warming, we may thus expect species
395 to live faster but die younger unless food becomes limiting.

396 The interacting effect of food and temperature on body size has also been demonstrated at
397 larger scales and in particular for trophic interaction strength, food chain persistence, and food web
398 stability (Sentis *et al.* 2014, Binzer *et al.* 2012, Binzer *et al.* 2016). Our results suggest that accounting
399 for life history trade-offs could be important to better understand the effect of global change on these
400 different levels of complexity. Furthermore, only body size reductions in adults were considered in
401 recent studies (Sentis *et al.* 2017, Osmond *et al.* 2017, Lindmark *et al.* 2018) while juveniles are larger
402 under warming. We emphasize the importance of proceeding investigations by considering ontogeny
403 in future studies as the temperature effect on growth are dependent on life stages. Bodner *et al.* (2021)
404 further demonstrated that larger species ontogeny can shape the structure of the communities. We
405 suggest that bioenergetic models such as the Dynamic Energy Budget (DEB) or Metabolic Theory of
406 Ecology (MTE) could be powerful to study the temperature-size-food relationships on individual
407 growth (Zuo *et al.* 2012) and survival. Indeed, these models can quantify the incoming and outgoing
408 flows of matter and energy while complying to the fundamental laws of thermodynamics (Kooijman
409 2000). It would thus be possible to investigate temperature and nutritional quantity and/or quality to
410 study their independent and interactive effects on energy allocation to maintenance, growth or
411 survival. Bioenergetics models coupled with population dynamics models, such as in Sentis *et al.*

412 (2022), show promise for studying how trade-offs at the individual level impact trophic interactions,
413 food webs and ecosystem processes under global change.

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418 Data, scripts and codes availability

419 Data, scripts and code are available online : <https://doi.org/10.6084/m9.figshare.20375850.v5>

420 Conflict of interest disclosure

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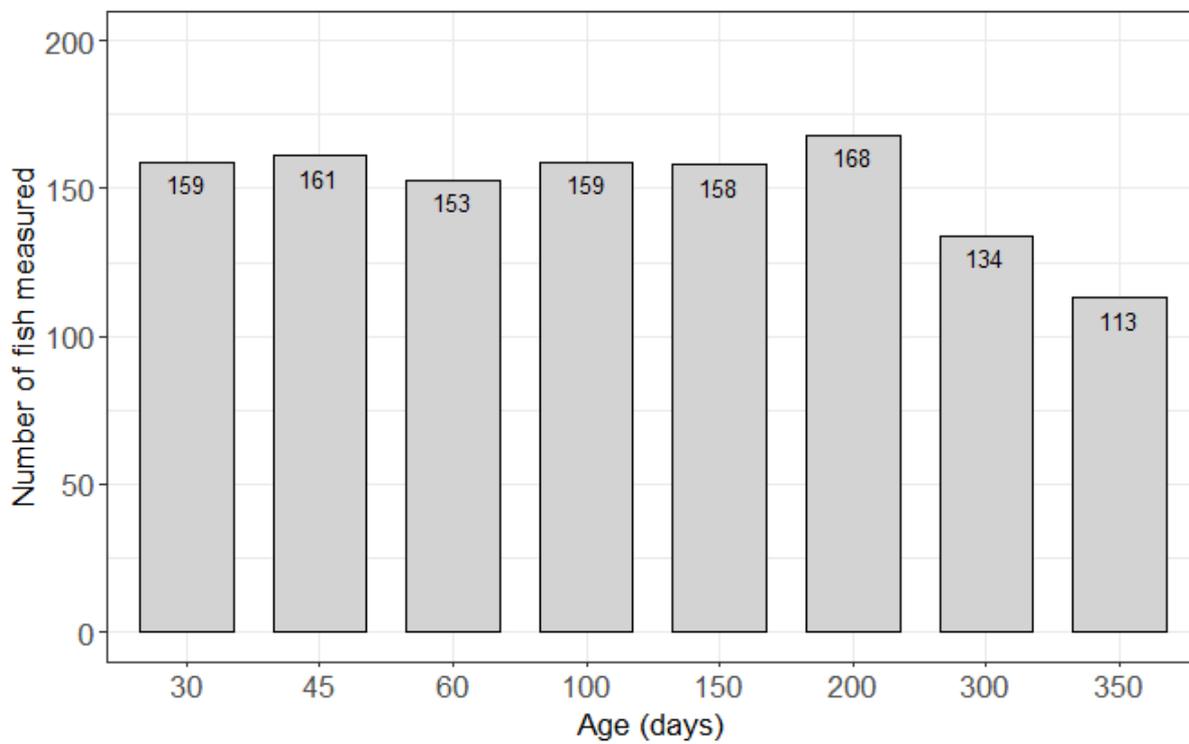
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686 Appendix

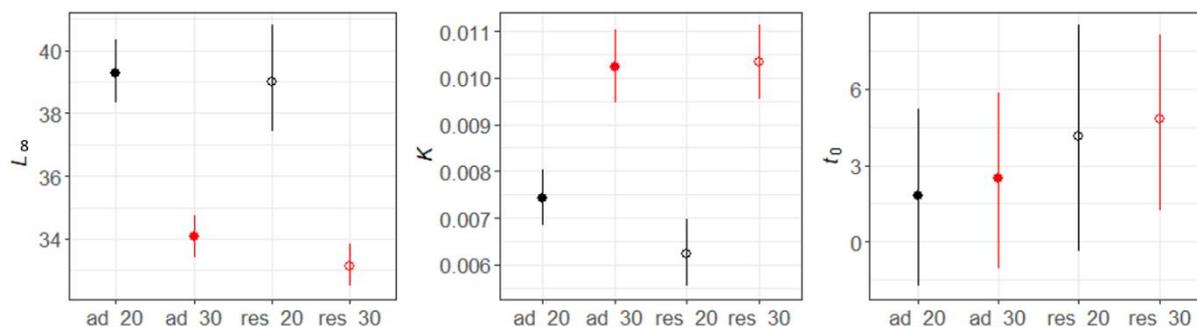
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Fig. S 1: Number of fish measured at different ages.



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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 *ad libitum* and food restriction treatments, respectively. Bars represent 95 % credibility intervals.

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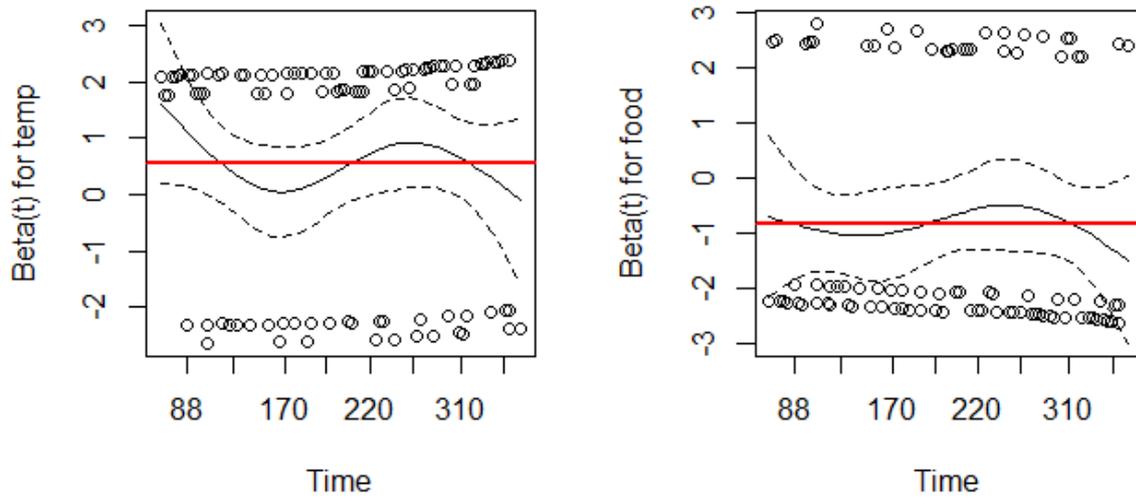
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Consistent with the experimental curves and TSR, warming significantly increased the initial growth rate K and decreased the maximum asymptotic size L_{∞} . Food restriction had no effect on the initial growth rate K for fish reared at 30 °C, but significantly 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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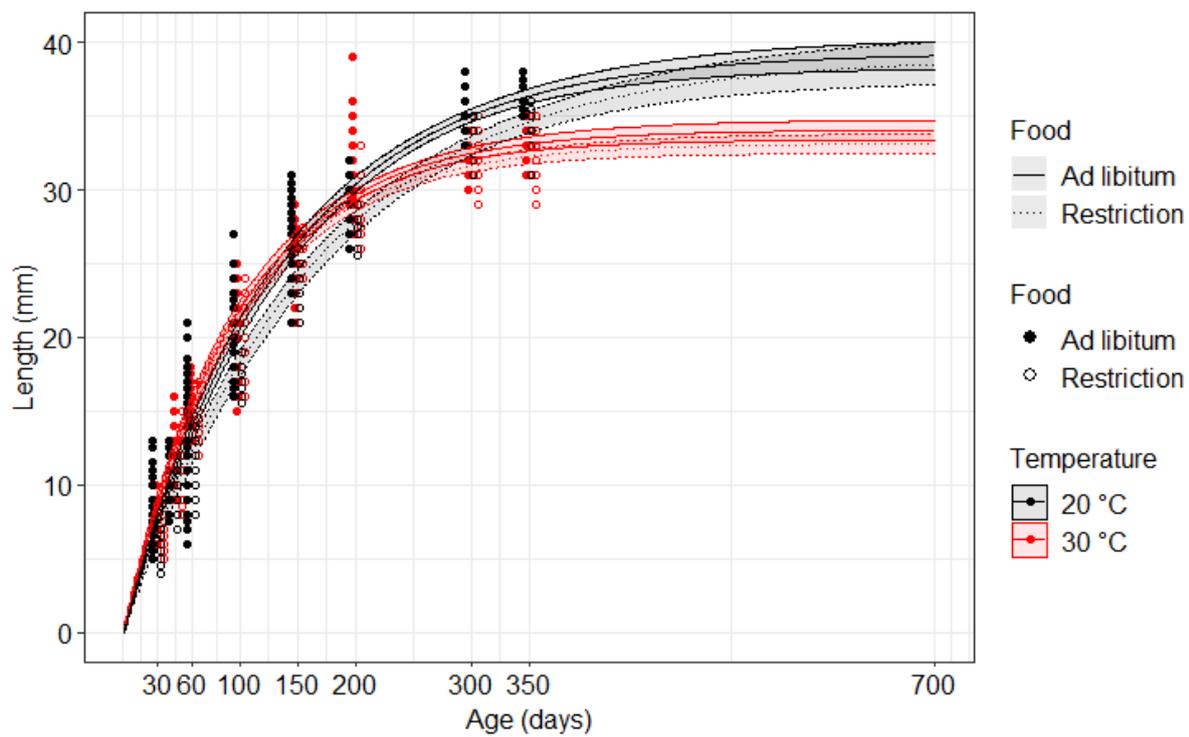
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The *cox.zph* function correlates the scaled Schoenfeld residuals with time for each covariate to test for independence between residuals and time. Additionally, it performs a global test for the model as a whole. From our model output, this test was 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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713 **Fig. S 4: Extrapolation of Von Bertalanffy growth curve for each combination of temperature and food conditions.**
 714 Black and red colors represent the cold and warm treatments, respectively. Solid and dotted lines represent the ad libitum
 715 and the food restriction treatments, respectively. Areas represent the 95 % credibility intervals.
 716 Points represent experimentally measured sizes at age.