

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

Simon BAZIN^{1,2,*}, Claire HEMMER-BREPSON², Maxime LOGEZ^{2,3}, Arnaud SENTIS² and Martin DAUFRESNE²

¹Univ. Savoie Mont Blanc, INRAE, CARRETEL, 74200 Thonon-les-Bains, France

²INRAE, Aix Marseille Univ., RECOVER, Aix-en-Provence, France

³INRAE, RIVERLY, F-69625, Villeurbanne Cedex, France

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

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 resourcefood availability isdoes not limitinglimit growth. Nevertheless, climate warming can decrease resourcefood availability by modifying biochemical cycles and primary production-. The interactive effects of temperature and it remains unclear if, food availability on life history traits have been studied in small invertebrate species, but we have limited information on how temperature and how, food availability jointly influence life history traits in vertebrate predators, despite the TSR pattern holds under resource restriction. Resource 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 the growth survival trade-off, although this remains untested 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 resourcefood 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. Resource restriction modulated this temperature effect, particularly by decreasing initial growth rate at 20 °C. Restricted Food-restricted fish were smaller than *ad libitum* fed fish throughout the experiment, leading to nested growth curves. ResourceIn addition, food restriction appears to amplify TSR by decreasing initial growth rate in the cold treatment and shrinking adult size in the warm treatment. The survival probability of fish was lower. Fish reared at 30 °C compared to 20 °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 where accelerated growth trades of with increased mortality. Resource under warming. Food restriction increased the survival probability under both temperature conditions corresponding to a "eat little die old" strategy when resource. Finally, food restriction decreases appeared to be advantageous as food restriction largely increased survival while have a weaker negative effect on growth but increases longevity and fecundity and no impact on age and size at maturity. Our results highlight the importance of accounting for the interaction between temperature and resourcefood 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

43 temperatures. Furthermore, we highlight the importance of considering ontogeny when investigating
 44 the effects of temperature-induced body size shifts on trophic interactions and community dynamics
 45 since thermal effects depend on the life stage of the organisms.

46 **Key-words:** climate change, resourcefood restriction, temperature, TSR, growth, survival, trade-
 47 offstrategy, life-history traits, fish.

48 Introduction

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

84 Besides temperature, another major factor underlying growth, reproduction and survival is
 85 resource ~~food~~ availability- (Boggs and Ross 1993, Giberson and Rosenberg 1992, Boersma and
 86 Vijverberg 1996, Corrêa et al. 2021). Individuals need enough resources, as energy and material inputs,
 87 to sustain their metabolic demand and optimize the allocation of energy to growth ~~and reproduction~~
 88 ~~(brown et al. 2004, Cross et al. 2015)~~. Interestingly, resource, reproduction and maintenance (Lemoine
 89 and Burkepile 2012, Brown et al. 2004, Cross et al. 2015). There is a long history of researches on the
 90 influence of food availability on the growth rate and fecundity of ectothermic species (Rasmussen and
 91 Ostenfeld 2000, Johnston et al. 2002, Giberson and Rosenberg 1992, Boersma and Vijverberg 1996,
 92 Corrêa et al. 2021). In most cases, individuals with a higher food availability have a higher fecundity
 93 and have both a higher initial growth rate and a larger asymptotic size compared to individuals under
 94 food restriction. In contrast to the pattern of crossed curves driven by temperature, different resource
 95 levels lead to a pattern of nested curves where the growth curve under limiting resources is nested
 96 below the growth curve under unlimited resources (Figure 1). Interestingly, food restriction may also
 97 be beneficial to the lifespan of organisms as this restriction reduces the production of senescence-
 98 accelerating oxidizing agents during metabolism (Sohal and Weindruch 1996, Gredilla et al. 2001,
 99 Speakman 2005), resulting in a “eat little die old” strategy. ~~There is a long history of researches on the~~
 100 ~~influence of resource availability on the growth rate of ectothermic species~~ (Rasmussen and Ostenfeld
 101 ~~2000, Johnston et al. 2002~~). ~~In most cases, individuals with a higher resource availability have both a~~
 102 ~~higher initial growth rate and a larger asymptotic size compared to individuals under resource~~
 103 ~~restriction. In contrast to the pattern of crossed curves driven by temperature, different resource levels~~
 104 ~~lead to a pattern of nested curves where the growth curve under limiting resources is nested below~~
 105 ~~the growth curve under unlimited resources (Figure 1)~~. ~~The effects of food restriction on fecundity~~
 106 ~~(which decreases) and survival probability (which increases) are thus opposite and can be explained by~~
 107 ~~a resources distribution to nutrient-limited processes~~ (Corrêa et al. 2021).

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

123 ~~Although the effects of food availability and temperature have been extensively studied~~
 124 ~~independently, the~~ The interactive effects of ~~these two factors remain relatively unknown. Only a few~~
 125 ~~studies have shown that resource quantity temperature and food availability on life history traits have~~
 126 ~~been studied in invertebrates such as daphnia~~ (Betini et al. 2020, ~~McLeod et al. 2013~~) Giebelhausen
 127 and quality (Lampert 2001, Wojewodzic et al. 2011, Persson et al. 2011) ~~can modulate the temperature~~

128 ~~effect on~~), aquatic insect larvae (Giberson and Rosenberg 1992) and terrestrial insects (Clissold and
 129 Simpson 2015, Corrêa *et al.* 2021, Stillwell *et al.* 2007, Kingsolver *et al.* 2006, Rohner *et al.* 2017). In
 130 these studies, warming generally resulted in a rapid life cycle by increasing growth rates and decreasing
 131 age and size at maturity as well as survival. However, these thermal effects were often modulated by
 132 food availability. For example, Betini *et al.* ~~in daphnia and fish~~. This is an important gap because, as
 133 explained above, temperature and resource (2020) found body size reduction under warming was five
 134 time stronger under limited food availability compared to unlimited conditions. Moreover,
 135 temperature and food availability can covary and impact ectotherm life history traits. Koussoroplis
 136 and Wacker (2016) showed that the effect of food restriction on life history traits is more severe when
 137 temperature moves away from the optimal temperature. Nevertheless, all the studies mentioned
 138 above were conducted on small invertebrate species. As a result, we have no information on how
 139 temperature and food availability jointly influence life history traits of vertebrate predators, despite
 140 the observation that TS responses are amplified in larger species (Forster *et al.* 2012). This is because
 141 of importance as body size changes in predatory species can alter the trophic interaction strength and
 142 food webs stability (Emmerson and Raffaelli 2004, Sentis *et al.* 2017, Osmond *et al.* 2017). We thus
 143 need to account for ~~must therefore consider~~ both the direct physiological impact of temperature as
 144 well as its indirect effects through modified resource/food availability on body size changes and life
 145 history traits of predatory species to better understand and predict the impacts/consequences of
 146 climate change on the growth-survival trade-off across trophic levels.

147 In this study, we address this gap by experimentally investigating growth, reproduction and
 148 survival of a ~~small Japanese fish~~ vertebrate predatory species, the medaka fish (*Oryzias latipes*,
 149 Temminck & schlegel), raised at two temperatures (20 and 30 °C) with and without resource/food
 150 restriction. Our objective was to test whether resource/TSR was maintained under food-restricted
 151 conditions and whether food restriction can modulate/modulated the effects of temperature on the
 152 growth and developmental strategies, fecundity and survival of a vertebrate predatory species. We
 153 expected warming to result in a rapid life style with faster growth but lower survival pattern of an
 154 ectotherm species, but these thermal effect would be modulated by food restriction, which increases
 155 survival and selects for late maturation at larger body size. We discuss the implication of our findings
 156 on (i) the importance of accounting for the temperature-resource/food interaction in the context of
 157 global warming, as we expect the quantity and nutritional quality of phytoplankton and zooplankton
 158 are modified by global warming (De Senerpont Domis *et al.* 2014) resources to change and (ii) to which
 159 extent investigating growth, reproduction and survival patterns could help disentangling the relative
 160 impacts of temperature and resources availability on body size shifts under global warming.

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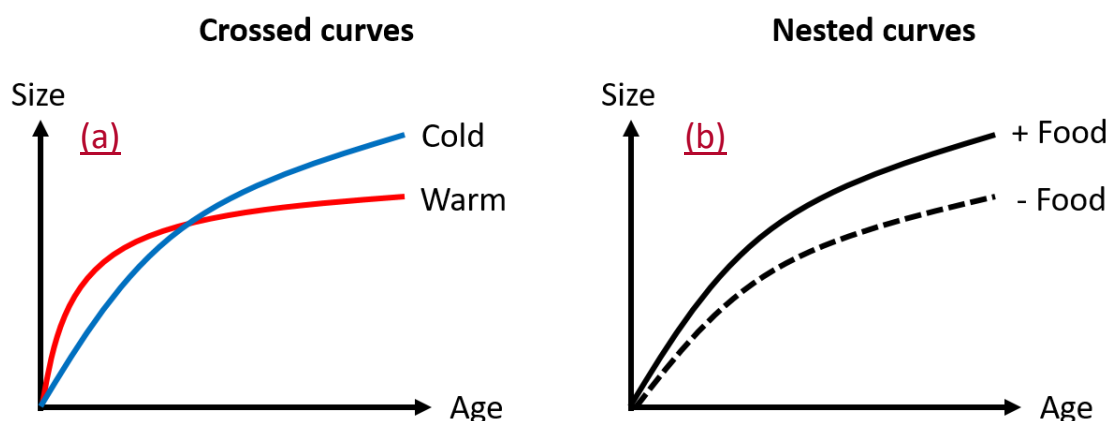


Figure 1: Patterns of crossed vs. nested growth curves driven by (a) temperature and (b) ~~resource~~food availability (after Berrigan and Charnov 1994).

Material and methods

Biological system and rearing conditions

The medaka is a small iteroparous freshwater fish native to East Asia (Hirshfield 1980). The life span of a medaka is about 2 years and its adult size varies between 30 and 50 mm (Ding *et al.* 2010, Egami and Etoh, 1969). This is an eurythermal species (5 °C - 35 °C) with an optimum ~~temperature~~temperature of 25 °C (Dhillon and Fox 2004). At this temperature, the medaka requires only 10 to 12 weeks to reach sexual maturity. Fish were maintained in the laboratory using an open water system with ~~water~~water supply controlled by drip emitters (1 L.h⁻¹). Input water quality was maintained with mechanical, biological and UV filtration with a pH of 7.5 at 16 °GH. Each tank (25 x 40 x 20 cm) was equipped with an air filter to prevent high nitrite concentrations and maintain oxygen at saturation.

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

From this F₀ generation, about 300 eggs were collected in each tank. Eggs were placed in small nurseries (2.5 L) made of fine mesh and each nursery was placed in the tank where the eggs were collected from (see Hemmer-Brepson *et al.* 2014, Loisel *et al.* 2019 for more details). After 30 days of growth, the parents were removed and the F₁ fish larvae were reared under four different treatment: ad_20 (*ad libitum* and 20 °C), res_20 (restriction and 20 °C), ad_30 (*ad libitum* and 30 °C) and res_30 (restriction and 30 °C). For each treatment, the growth of approximately 80 fish was ~~monitored~~monitored, except for res_20 where only 54 fish could be maintained. Fish were maintained in 20 L aquaria

194 with 20 - 30 fish of a single treatment. This density (less than 2 - 3 fish per liter) does not cause any
 195 stress or agonistic behaviour in this species (Denny *et al.* 1991). The fish were fed with TetraMin[®]
 196 (composition: 47 % protein, 10 % fat content, 3 % cellulose and 6 % water) every morning (for the *ad*
 197 *libitum* condition) or every two mornings (for the restriction condition). On each feeding days,
 198 TetraMin[®] was provided to each tank until the fish no longer went up to the surface to get food. Excess
 199 food was systematically removed after feeding to prevent feeding between two meals. Apart from
 200 temperature and ~~resource~~food, all the experimental parameters were similar in the four ~~treatments.~~
 201 treatments.

202

203 ~~Growth~~measurement, fecundity and survival

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205 The total length (from the head to the tip of the caudal fin, TL) of each fish was measured with
 206 a precision of 0.5 mm at 30, 45, 60, 100, 150, 200, 300 and 350 days. Fish were measured after placing
 207 them on a 5 cm diameter Petri dish layered with a millimeter graph paper and filled with ~~water~~water.
 208 They were then immediately released into their respective tank. An average of 150.6 ± 18.1 fish were
 209 measured per age (see ~~Fig. S 1~~Fig. S 1 for more details). As fish were not ~~identify~~identified individually,
 210 the growth curves applies to the experimental population (i.e. one curve per treatment) and not to
 211 ~~individuals~~individuals. ~~The investment in reproduction was quantified from sexual maturity by~~
 212 counting the number of eggs laid per female per day in each tank. Survival was monitored daily from
 213 ~~65~~60 days (age of first sexually mature fish) until the end of the experiment.

214 Statistical analysis

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

$$218 \quad L_t = L_\infty (1 - e^{-k(t-t_0)}) \quad \text{--- (eq. 1) (eq. 1) ---}$$

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

222 Von Bertalanffy growth curves parameters (L_∞ , K , t_0) were estimated by Bayesian inference
 223 using the Bayesian software JAGS and the "R2jags" package (Su and Yajima, 2015) in R software
 224 (version 4.0.2; R development Core Team). We assumed that the asymptotic size L_∞ , ~~and~~ the initial
 225 growth rate K , and the theoretical age at null size t_0 could vary between temperature (T) and resource
 226 (C) condition, ~~while the theoretical age at null size t_0 , could only vary with temperature and not with~~
 227 ~~resource condition as resource restriction started after egg hatching (when fish larvae were 30 days~~
 228 ~~old).~~ Consequently, four values of L_∞ , K and Kt_0 (one for each combination (CT) of temperature and
 229 resource condition) were fitted ~~and only two values of t_0 were fitted, one for each temperature~~. For
 230 each parameter, we used a normal uninformative prior with a mean of 0 and a precision parameter
 231 (inverse of the variance) ~~Gamma distributed (scale and rate of 0.001):~~

$$\begin{aligned}
 & \frac{L_{\infty CT} N(0, \sigma_{L_{\infty}})}{\sigma_{L_{\infty}} = \frac{1}{\sqrt{\tau_{L_{\infty}}}}}; \quad \frac{K_{CT} N(0, \sigma_K)}{\sigma_K = \frac{1}{\sqrt{\tau_K}}}; \quad \frac{t_{0CT} N(0, \sigma_{t_0})}{\sigma_{t_0} = \frac{1}{\sqrt{\tau_{t_0}}}} \quad (\text{eq. 2}) \\
 & L_{\infty CT} \sim N(0, 0.001) \quad K_{CT} \sim N(0, 0.001) \quad t_{0CT} \sim N(0, 0.001) \\
 & \tau_{L_{\infty}} \sim \Gamma(0.001, 0.001) \quad \tau_K \sim \Gamma(0.001, 0.001) \quad \tau_{t_0} \sim \Gamma(0.001, 0.001)
 \end{aligned}$$

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

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

236 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
 237 correlations between these vectors. We used uninformative priors with a uniform distribution for each
 238 parameter of Σ , adapting the limits to the parameters (e.g between -1 and 1 for a correlation).

239 $L_{\infty CT}, K_{CT}$ and t_{0CT} are thus hyperpriors (population parameters) that serve to assess parameters for
 240 each tank (t) when associated with the random effects. For instance for the L_{∞} parameter:

$$241 \quad L_{\infty t} = L_{\infty CT} + \varepsilon_{L_{\infty} t} \quad (\text{eq. 4})$$

242 We then used (eq. 1) to estimate the expected mean total length L_{tj} for each fish (j), depending of
 243 its tank (t), and each age (t_j) and its temperature and resource condition (j):

$$244 \quad L_{tj} = L_{\infty CT} \left(1 - e^{-k_{CT}(t_j - t_{0CT})} \right) \quad (\text{eq. 3})$$

$$245 \quad L_{tj} = L_{\infty t} \left(1 - e^{-k_t(t_j - t_{0t})} \right) \quad (\text{eq. 5})$$

246 Finally, we hypothesized that the observed total length of each fish, $L_{tj}(f)$, was normally distributed:

$$\begin{aligned}
 & \frac{L_{tj} N(L_{tj}, \sigma)}{\sigma = \frac{1}{\sqrt{\tau_{L_{tj}}}}} \quad (\text{eq. 4}) \\
 & \tau_{L_{tj}} \sim \Gamma(0.001, 0.001)
 \end{aligned}$$

$$248 \quad \begin{aligned}
 & L_{tj} \sim N(L_{tj}, \sigma) \quad (\text{eq. 6}) \\
 & \sigma \sim U(0, 10)
 \end{aligned}$$

249 To compare the growth patterns among temperature and resource conditions, we plotted the average
 250 growth curves (eq. 3) for each treatment (combination of food condition and temperature), and their
 251 credible interval (CI) using the posterior distributions of the parameters ($L_{\infty}, K, t_{0CT}, K_{CT}, t_{0CT}$)
 252 that were obtained from five independent Monte-Carlo Markov Chains (see Fig. S 2 Fig. S 2 for more
 253 details on the estimated parameter values). For each chain, after an initial burning of 50 000 values,
 254 200 000 iterations were computed and we conserved one value every 1000 iterations to limit
 255 autocorrelation between estimations. The posterior distributions for each average total length at age
 256 (L) were thus constituted of 10,000 values. The quantiles 2.5 % and 97.5 % were used to estimate
 257 credibility intervals CIs. We compared the growth curves among our four experimental treatments by
 258 investigating the overlap among their CIs. Curves were considered as significantly different when their
 259 CIs do not overlap (Pritchard *et al.* 2017).

260 We investigated the effects of temperature, ~~resource~~food restriction and their interaction
261 (fixed effects) on mean daily clutch size per female (log transformed) and survival probability using a
262 linear mixed effects model (*lmer* function in the “lme4” package (Bates *et al.* 2015)) and a mixed effects
263 Cox proportional hazards model (~~*coxph*~~*coxme* function in the “~~survival~~*coxme*” package (Therneau *et*
264 *al.* 2022)) ~~followed by a variance analysis (anova.)~~), respectively, with tank as random factor. For both
265 models, analyses of deviance using Wald tests were provided to test the significance of fixed
266 parameters. We tested the assumptions of the mixed effects Cox ~~model~~ proportional hazards
267 assumption using the Global test statistic from model using the *cox.zph* function (“survival” package
268 (Therneau *et al.* 2022)) which correlates the corresponding set of scaled Schoenfeld residuals with time
269 to test for independence between residuals and time (see ~~Fig. S 3~~**Fig. S 3** for more details).

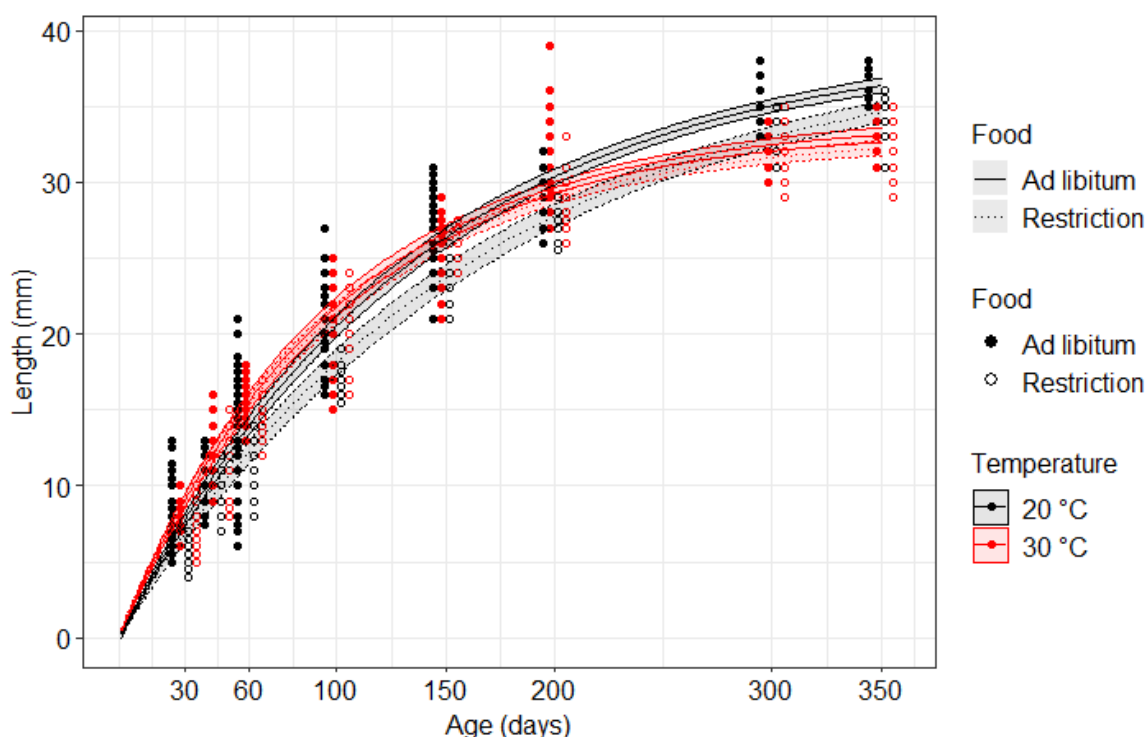
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271 Results

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273 We found that, at both resourcefood conditions, warming leads to crossed growth curves by
 274 increasing initial growth rate and decreasing adult size, although the curves crossed later for the
 275 resourcefood-restricted fish (Figure 2). ResourceFood restriction in the cold treatment leads
 276 to nested growth curves throughout the experiment by decreasing the initial growth rate and adult
 277 size. Growth curves are also tended to be nested over almost the entire experiment in the warm
 278 treatment (Figure 2). although the credibility intervals overlapped until day 220 and the curves were
 279 only significantly different toward the end of the experiment (from day 220 to day 300, Figure 2).

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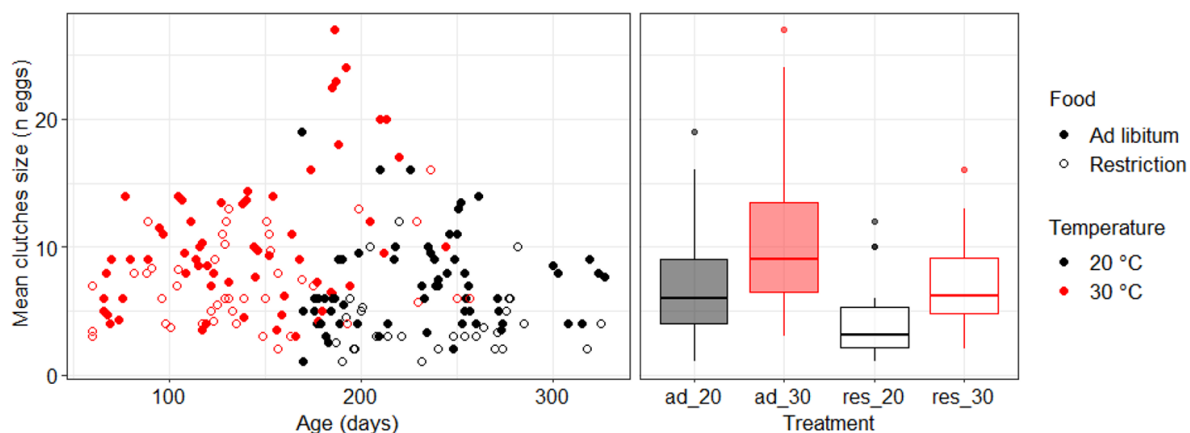
282 **Figure 2: Fitted von Bertalanffy growth curve for each combination of temperature and resourcefood conditions.**

283 Blue/Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively. Solid and dotted lines
 284 represent the ad libitum and the resourcefood restriction treatments, respectively. Areas represent the 95 % credibility
 285 intervals.

286 JitteredAs fish were not identified individually, jittered points represent experimentally measured sizes (in mm) at age (in
 287 days) of fish from different replicates (i.e.tanks).

288 In the warm treatment, the fish were sexually mature at 67.3 ± 2.3 days (body length: $16.8 \pm$
 289 0.1 mm) under ad libitum condition and at 60 days for all replicates (body length: 17.2 ± 0.7 mm) under
 290 food restriction. In the cold treatment, they were sexually mature at 169.7 ± 0.6 days (body length:
 291 26.3 ± 0.6 mm) and 186.5 ± 0.7 days (body length: 25.7 ± 0.4 mm) under ad libitum and food restriction
 292 conditions, respectively (Figure 3). We found that warming increased mean daily clutch size per female
 293 ($df = 1$, $Chi^2 = 13.26$, $p < 0.001$) and food restriction decreased it ($df = 1$, $Chi^2 = 10.58$,
 294 $p = 0.001$). Mean daily clutch size per female was not dependent on the interaction between
 295 temperature and food conditions ($df = 1$, $chi^2 = 0.79$, $p = 0.37$).

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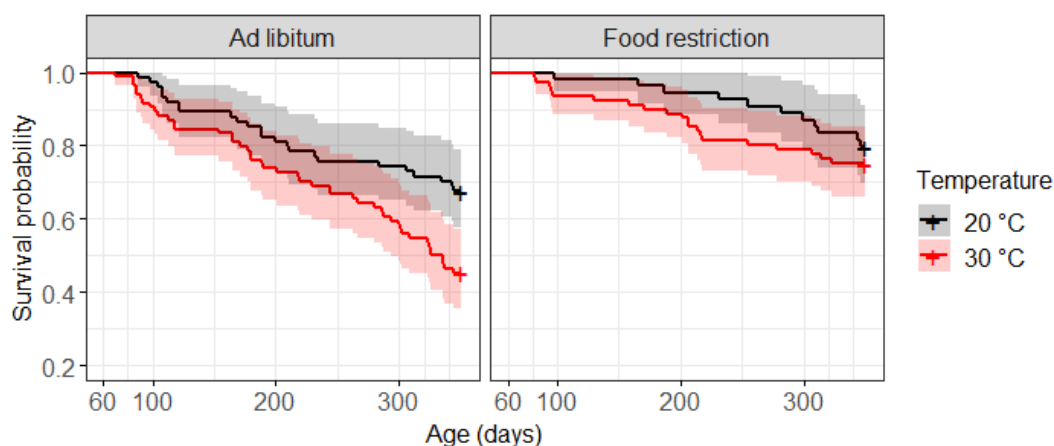
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Figure 3: Temperature and food restriction effects on mean daily clutch size per female.
Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively.
Filled and empty points and boxplot represent the ad libitum and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

The fish survival probability was not significantly affected by the interaction between warming and **resourcefood** restriction ($\chi^2 = 0.6970$, $df = 1$, $p = 0.4140$, $n = 292$). In contrast, warming significantly reduced the fish survival probability ($\chi^2 = 7.29$, $df = 1$, $p = 0.01$, $n = 292$). Moreover, **resourcefood** restriction significantly increased survival probability ($\chi^2 = 16.34$, $df = 1$, $p < 0.001$, $n = 292$) (Figure 4).



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314 Discussion

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Body size is a key trait in ecology as it affects many biological and ecological properties ranging from the individual to the ecosystem. Body size influences metabolism, fecundity, trophic position,

318 locomotion, trophic interactions, or food web persistence and stability (Peters 1986, Calder 1996,
 319 Brown *et al.* 2004, Gibert and Delong, 2014, Sentis *et al.* 2017, Emmerson and Raffaelli 2004, Osmond
 320 *et al.* 2017, Lindmark *et al.* 2018). Shrinking body size with increasing temperature has been proposed
 321 as a third universal response to global warming (Daufresne *et al.* 2009, Gardner *et al.* 2011). In addition,
 322 the quantity and quality of resources are expected to change with global warming (De Senerpont
 323 Domis *et al.* 2014), in response to changes in physicochemical, phenological (Visser and Both, 2005)
 324 and geographical parameters (Parmesan and Yohe, 2003). ~~Although the~~The independent and
 325 interactive effects of temperature and ~~resource-food availability~~ on ~~growth and survival~~life history
 326 traits have been ~~largely~~mainly studied ~~independently~~ (Daufresne in small aquatic (Betini *et al.* 2020,
 327 Giebelhausen and Lampert 2001, Wojewodziec *et al.* 2011, Persson *et al.* 2009–2011, Giberson and
 328 Rosenberg 1992) and terrestrial (Clissold and Simpson 2015, Corrêa *et al.* 2021, Stillwell *et al.* 2007,
 329 Rohner *et al.* 2017) invertebrate species. However, we have no information on how temperature and
 330 food availability jointly influence life history traits in vertebrate predators, despite the observation that
 331 TS responses are amplified in larger species (Forster *et al.* 2012, Rasmussen and Ostefeld 2000,
 332 Johnston *et al.* 2002), the interactive effects of these two factors on the growth-survival trade-off
 333 remain relatively unknown, despite its potential implications for community dynamics and interspecific
 334 interactions (Werner and Anholt 1993.) and that body size reduction at higher trophic level can
 335 increase food web persistence at high temperature (Sentis *et al.* 2017). Our objective was thus to test
 336 whether ~~resource~~food availability can modulate the effects of temperature on ~~the~~ size at age ~~growth~~
 337 and ~~survival~~patternlife history traits of a ~~common fish used in labs~~vertebrate predator species, the
 338 medaka- fish.

339 The results of our laboratory experiment indicate that, in agreement with the TSR rule
 340 (Atkinson and Sibly 1997, Berrigan and Charnov 1994, Arendt 2011), warming leads to crossed growth
 341 curves with individuals growing faster but reaching a smaller adult size compared to the cold condition.
 342 The ecological consequences of temperature-induced changes in body size are multiple. This would
 343 result in changes in the predator-prey size ratio and because body size potentially determines prey
 344 size, this has important implications for predator-prey and community dynamics (Sentis *et al.* 2017,
 345 Yodzis and Innes 1992, Kalinkat *et al.* 2013, Vagnon *et al.* 2021). On a larger scale, the structuring
 346 effects of body size in food webs have been widely demonstrated (Williams and Martinez 2000,
 347 Emmerson and Raffaelli 2004). Size interacts with temperature because temperature alters the
 348 energetic demands of organisms, and thus also alters the strength of trophic interactions. For example,
 349 higher temperature has been shown to increase short-term predator-prey interaction strength and
 350 predator energetic efficiency (Sentis *et al.* 2012). These different studies illustrate the importance of
 351 considering size and temperature in studies of global warming effects. To date, studies examining the
 352 consequences of temperature-induced body size shifts on trophic interactions, community dynamics,
 353 and food web structure, only considered the reduction in adult size (Sentis *et al.* 2017, Osmond *et al.*
 354 2017, Lindmark *et al.* 2018). ~~However, warming leads to larger juvenile but smaller adults and~~
 355 ~~thus~~However, a recent study showed that effects of mass and temperature on metabolism are
 356 interacting such that the effect of temperature varies between large and small fish (Rubalcaba *et al.*
 357 2020), suggesting that the impacts of temperature-induced body size shifts on ecosystem functioning
 358 certainly depends on life stages. Lindmark *et al.* (2022) investigated the effects of temperature on
 359 individual growth rates and size structure in a food web context and suggest that both direct metabolic
 360 effects and indirect effects of temperature via basal resources need to be considered to understand
 361 how global warming affects community size structure.

362 Furthermore, size and temperature alter the metabolism and energy requirements of
 363 organisms (Brown *et al.* 2004) which implies that resourcefood also plays a crucial role in the overall
 364 responses of aquatic ecosystems to climate warming (Ruiz *et al.* 2020). In our study, despite the curves
 365 being nested throughout the experiment ~~at both temperatures~~ in agreement with previous studies
 366 (Rasmussen and Ostensfeld 2000, Johnston *et al.* 2002), the resourcefood restriction effects appeared
 367 to be greater at 20 °C where the curves were more nested than at 30 °C. This is surprising because we
 368 expected resourcefood restriction to have more effect at 30 °C (as shown in McLeod *et al.* 2013,
 369 Wojewodziec *et al.* 2011, and Persson *et al.* 2011) because warming increases metabolic rates which
 370 implies higher energy demand and feeding rate to sustain high metabolic costs (Brown *et al.* 2004).
 371 ~~Our result is in line with recent studies investigating the interactive effects of temperature and~~
 372 ~~resource availability on aquatic organisms such as daphnia (Wojewodziec *et al.* 2004).~~ For instance,
 373 Wojewodziec *et al.* (2011) and Persson *et al.* (2011) reported that warming further amplifies the
 374 decrease in somatic growth rates of Daphnia under low nutritional quality (high C:P ratio) compared
 375 to Daphnia under high nutritional quality (low C:P ratio). ~~2011, Persson *et al.* 2011, Betini *et al.* 2020~~
 376 ~~and fish (McLeod *et al.* 2013). For example, Betini *et al.* 2020 showed that the reduction in body size~~
 377 ~~induced by temperature was greater under low resources conditions. Similar results were observed in~~
 378 ~~Amphiprion percula larvae, where low resource availability limited growth rates in warm condition~~
 379 ~~(McLeod *et al.* 2013). Wojewodziec *et al.* (2011) and Persson *et al.* (2011) reported that somatic growth~~
 380 ~~rates of daphnia decrease as C:P ratios in resources increase, and that this effect is amplified under~~
 381 ~~warming.~~ These results suggest that temperature-induced body size shifts depend on the quantity but
 382 also the quality of resources with lower resource quality amplifying the detrimental effect of warming
 383 as reported in a recent study (Sentis *et al.* 2022). In our study, based on the full growth curves, food
 384 restriction therefore appears to amplify TSR by decreasing initial growth rate in the cold treatment, as
 385 suggested by Cross *et al.* (2015). Betini *et al.* (2020) also found a TSR amplification under food
 386 restriction as the body size reduction under warming was five times stronger under food restricted
 387 conditions than under unlimited food conditions. Recent studies have also shown that TSR tends to be
 388 amplified under oxygen limitation, which can be also considered as a limiting resource (Frazier *et al.*
 389 2001, Hoefnagel and Verberk 2015, Verberk *et al.* 2021). Nevertheless, TSR is not exclusively defined
 390 by adult size, but is also frequently assessed by size at maturity (Hoefnagel and Verberk 2015, Walters
 391 *et al.* 2006, Verberk *et al.* 2021). Focussing on size at maturity is more relevant to assess the influence
 392 of food restriction on evolutionary strategies as it is a better determinant of fitness than asymptotic
 393 size (Verberk *et al.* 2021). When considering size at maturity, food restriction did not appear to amplify
 394 TSR in our study as, at each temperature, fish reached sexual maturity at a similar age and size. This
 395 suggests that food restriction would not influence medaka's fitness via its effects on developmental
 396 time and size at maturity. A recent study also indicates that organism's evolutionary responses to
 397 warming can mitigate food restrictions, thereby avoiding constraints on whole-organism growth
 398 (Verberk *et al.* 2021). For example, organisms can increase the surface area for resource uptake by
 399 altering body shape, increasing organ surface area, or modulating feeding activity or locomotion
 400 (Verberk *et al.* (Wojewodziec *et al.* 2011, Persson *et al.* 2011)-2021).

401 For several species, warming leads to early maturation, smaller size, and increased fecundity
 402 (Betini *et al.* 2020, Marn *et al.* 2017). Our results are in line with these studies as we found that fish
 403 reared at 30 °C were sexually mature at a younger age, were smaller at maturity and produced a larger
 404 mean daily clutch size per female. In contrast, less is known about the responses of developmental
 405 rates and fecundity to covariation between temperature and food. Our results did not suggest any

406 effect of food restriction on age and size at maturity, in contrast to Betini *et al.* (2020) and Marn *et al.*
 407 (2017), who found that increased food availability resulted in earlier maturation. However, we found
 408 that food restriction decreased mean daily clutch size at both temperature conditions. Several studies
 409 have also found that increased food availability increased fecundity in both aquatic (Betini *et al.* 2020,
 410 Giberson and Rosenberg 1992) and terrestrial (Corrêa *et al.* 2021) organisms. This can be explained by
 411 an increase in the amount of energy to be allocated to reproduction under unlimited food conditions.

412 In addition, the survival probability of fish in our experiment was influenced by both
 413 temperature and resourcefood restriction. Indeed, fish reared at 30 °C had a lower survival probability
 414 than fish reared at 20 °C while resourcefood restriction increased the survival probability under both
 415 temperature conditions. This beneficial effect of resourcefood restriction on survival probability was
 416 also observed in frog larvae (Courtney Jones *et al.* 2015) and daphnia (Betini *et al.* 2020). Lower
 417 resourcefood availability implies a decrease in metabolism and thus a lower production of oxidizing
 418 agents which contributes to slow down senescence and increase survival probability after maturity,
 419 resulting in a "eat little die old" strategy (Sohal and Weindruch, 1996, Gredilla *et al.* 2001, Speakman
 420 2005, Pifferi *et al.* 2018). Our results potentially illustrates different developmental strategies. For
 421 example, at 30 °C, fish may have maintained a high growth rate despite resourcefood restriction in
 422 order to maintain a rapid life cycle, at the expense of lower survival. This hypothesis is supported by
 423 the fact that mortality was higher and sexual maturity was reached at a younger age ~~(65 days at 30 °C~~
 424 ~~against 160 days at 20 °C, unpublished data) and smaller size (17 mm at 30 °C against 26.5 mm at 20~~
 425 ~~°C, unpublished data) at 30 °C and smaller size at 30 °C compared to 20 °C.~~ This strategy is commonly
 426 referred to as "live fast die young strategy" (Bestion *et al.* 2015). Ultimately, measuring the fitness of
 427 the fish under the different conditions would help understanding if these two strategies (i.e. eat little
 428 die old and live fast die young) are adaptive or results from physiological constraints than are difficulty
 429 overpassed by evolutionary adaptations.

430 ~~Resource-restricted fish were smaller than *ad libitum* fed fish. Thus, in our study,~~
 431 ~~resourceAlthough food~~ restriction ~~appears to amplify~~ decreased the mean daily clutch size and
 432 ~~amplified~~ TSR by decreasing ~~the~~ initial growth rate and adult size in the cold and warm treatments,
 433 ~~respectively. Cross *et al.* (2015) suggested that the warming effects on growth could be amplified by~~
 434 ~~low resource availability, particularly in single-celled organisms such as algae and bacteria, because~~
 435 ~~small cells tend to have lower nutritional requirements and increased nutrient acquisition compared~~
 436 ~~to large cells (Cross *et al.* 2015). A recent study tested this hypothesis by investigating the warming~~
 437 ~~effects on protist growth under the influence of different resource availability and interspecific~~
 438 ~~competition (Tan *et al.* 2021). The warming effects on body size were not exacerbated by low resource~~
 439 ~~availability or high interspecific competition. Instead, the authors found that interspecific competition~~
 440 ~~elongates the body shape of protists, increasing their swimming speed and resource acquisition ability,~~
 441 ~~potentially making up for low resource availability (Tan *et al.* cold conditions, these effects 2021).~~
 442 ~~Another recent study also indicates that organism's evolutionary responses to warming can mitigate~~
 443 ~~resource restrictions, thereby avoiding constraints on whole organism growth (Verberk *et al.* 2020).~~
 444 ~~For example, organisms can increase the surface area for resource uptake by altering body shape,~~
 445 ~~increasing organ surface area, or modulating feeding activity or locomotion (Verberk *et al.* 2020).~~
 446 ~~Although our results suggest that TSR was amplified by resource restriction, the effects of resource~~
 447 ~~restriction were relatively weak: compared to the increase in survival probability.~~ This may therefore
 448 be explained by potential acclimation of medaka to rearing temperatures or by a resourcefood
 449 restriction being not sever enough. ~~The resource provided to the fish was not weighed for convenience~~

450 ~~and logistic limitations.~~ Reducing feeding events by half (1 out of 2 mornings) was considered
 451 restrictive ~~and significantly affected survival. However, resource restriction did not appear to be strong~~
 452 ~~enough to observe a significant effect on adult fish size at 30 °C. Resource effects~~ although we cannot
 453 exclude compensatory mechanisms were restricted fish would feed more when they have access to
 454 food.

455 ~~Overall, we found that temperature significantly increased initial growth rate and decreased~~
 456 ~~adult size leading to crossed growth curves, consistent with TSR. Resource restriction led to nested~~
 457 ~~growth curves, but the effects appeared to be greater at 20 °C. Resource restriction thus appears to~~
 458 ~~amplify TSR by decreasing initial growth rate and adult size in the cold and warm treatments,~~
 459 ~~respectively. To our knowledge, this is the first experiment showing that resource restriction amplified~~
 460 ~~TSR in fish. The results of this experiment demonstrate~~ Although this remains to be investigated in
 461 more details, our results highlight the importance of considering the interactions between
 462 temperature, body size and ~~resource.~~ Moreover, we found a trade-off between growth and survival
 463 with accelerated growth but lower survival under warming. Resource food to understand how larger
 464 predatory species respond to global changes in terms of developmental and life history strategies.
 465 Indeed, warming resulted in a rapid life style and increased fecundity at the cost of lower survival
 466 probability. However, food restriction modulated ~~this trade-off by decreasing growth and increasing~~
 467 ~~survival.~~ the effects of temperature and ultimately appeared to be evolutionarily advantageous since
 468 its positive effects on survival were accompanied by a weak decrease in growth and fecundity, and did
 469 not impact developmental times. Under warming, we may thus expect species to live faster but die
 470 younger unless resource food becomes limiting. ~~As a consequence, the final outcome will depends on~~
 471 ~~how temperature changes relative to resource availability.~~

472 The interacting effect of resource food and temperature on body size has also been
 473 demonstrated at larger scales and in particular for trophic interaction strength, food chain persistence,
 474 and food web stability (Sentis *et al.* 2014, Binzer *et al.* 2012, Binzer *et al.* 2016). Our results suggest
 475 that ~~accounting~~ accounting for life history trade-offs could be important to better understand the effect
 476 of global change on these different levels of complexity. Furthermore, only body size ~~reduction~~
 477 ~~was~~ reductions in adults were considered in recent studies (Sentis *et al.* 2017, Osmond *et al.* 2017,
 478 Lindmark *et al.* 2018) while juveniles are larger under warming. We emphasize the importance of
 479 proceeding investigations by considering ontogeny in future studies ~~since~~ as the temperature effect on
 480 growth are dependent on life stages. Bodner et al. (2021) further demonstrated that larger species
 481 ontogeny can shape the structure of the communities. We suggest that bioenergetic models such as
 482 the Dynamic Energy Budget (DEB) or Metabolic Theory of Ecology (MTE) could be powerful to study
 483 the temperature-size-resource food relationships on individual growth (Zuo *et al.* 2012) and survival.
 484 Indeed, these models can quantify the incoming and outgoing flows of matter and energy while
 485 complying to the fundamental laws of thermodynamics (Kooijman 2000). It would thus be possible to
 486 investigate temperature and nutritional quantity and/or quality to study their independent and
 487 interactive effects on energy allocation to maintenance, growth or survival. Bioenergetics models
 488 coupled with population dynamics models, such as in Sentis *et al.* (20202022), show promise for
 489 studying how trade-offs at the individual level impact trophic interactions, food webs and ecosystem
 490 processes under global change.

491

492 Acknowledgements

493 We thank the technical team and all people involved in the laboratory experiment for their help with
 494 fish rearing. [We thank the recommender Aleksandra Walczyńska and the reviewers Wolf Blanckenhorn](#)
 495 [and Wilco Verberk for their insightful comments that helped to improve the manuscript quality.](#)

496 Data, scripts and codes availability

497 Data, scripts and code are available online : <https://doi.org/10.6084/m9.figshare.20375850.v4v5>

498 Conflict of interest disclosure

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

501 Funding

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

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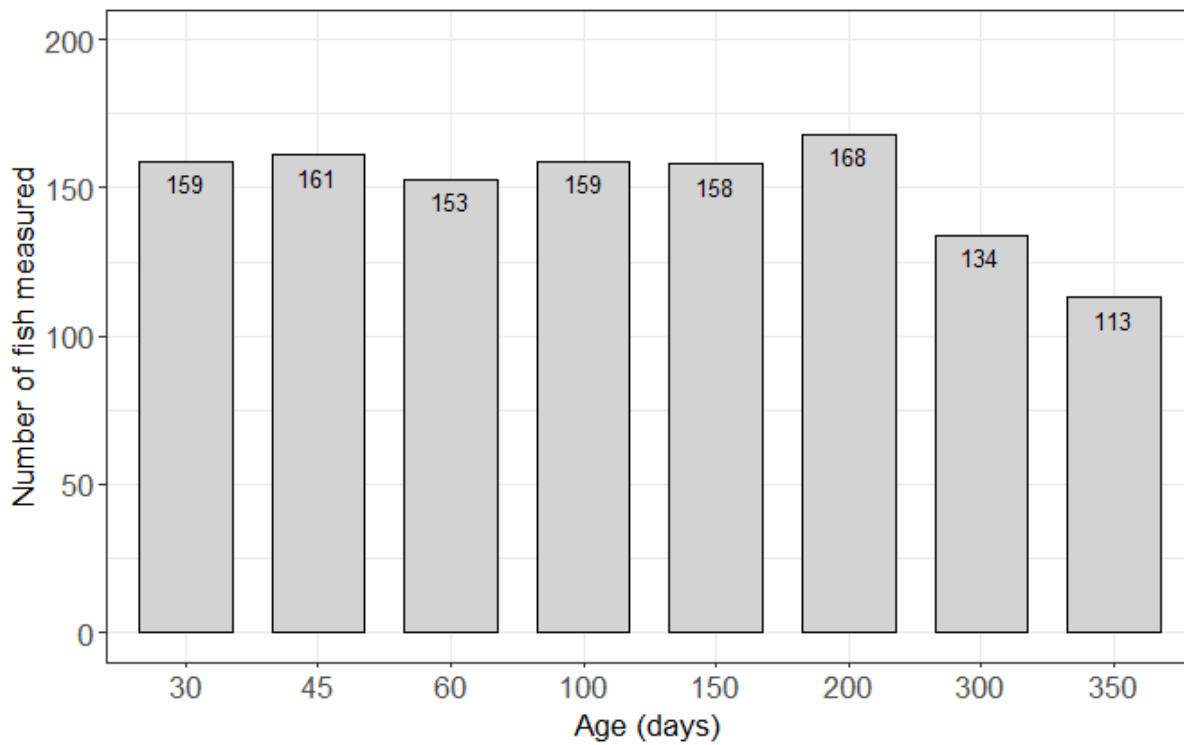
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769 Appendix

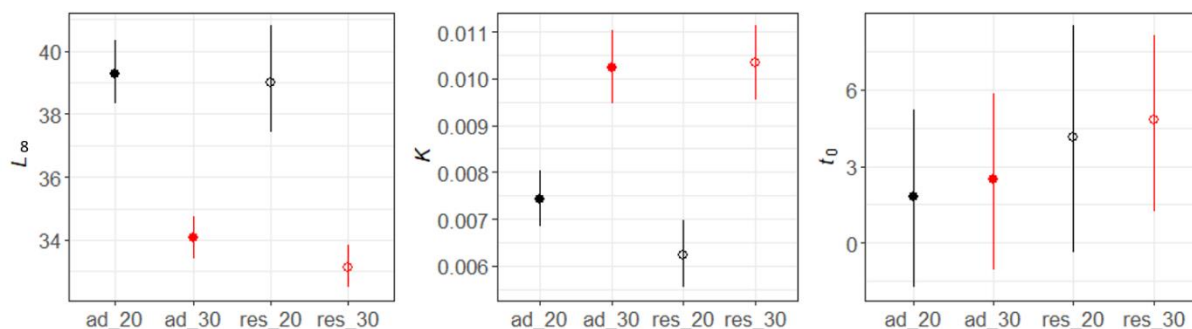
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Fig. S 1: Number of fish measured at different ages.



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

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BlueBlack and red colors correspond to the cold and warm treatments, respectively. CirclesFilled and trianglesempty circles correspond to the ad libitum and resourcefood restriction treatments, respectively. Bars represent 95 % credibility intervals.

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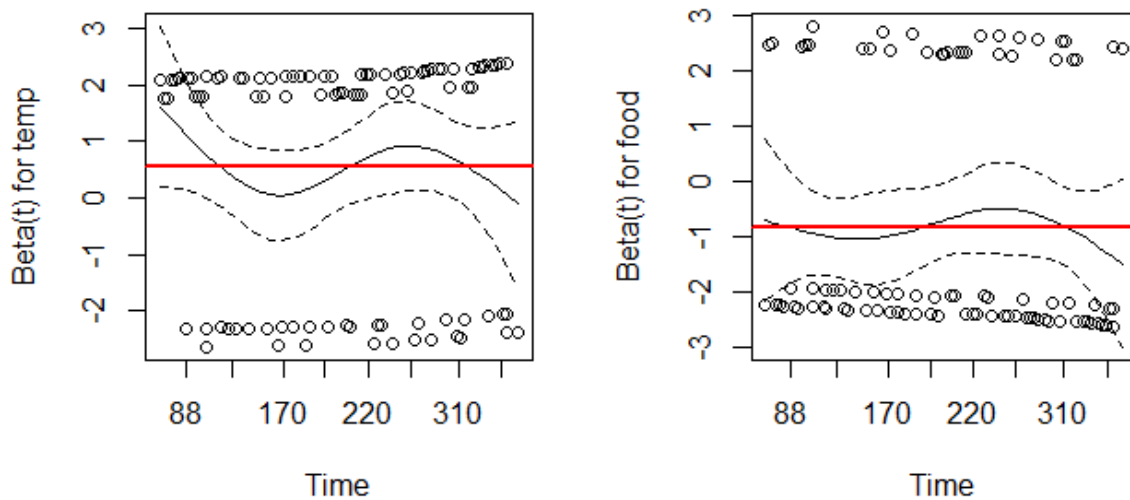
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Consistent with the experimental curves and TSR, warming significantly increased the initial growth rate K and decreased the maximum asymptotic size L_{∞} . ResourceFood restriction had no effect on the initial growth rate K for fish reared at 30 °C, but significantly reduced K for fish reared at 20 °C. At the end of our experiment, the adult size of resourcefood restricted fish was smaller than that of ad libitum fed fish, especially at 20 °C. Yet, resourcefood 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 resourcefood 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 320300 days under cold and warm conditions, respectively (Fig. S 4 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. 5.3: Cox model assumption of proportionality for temperature and **resourcefood** condition.*

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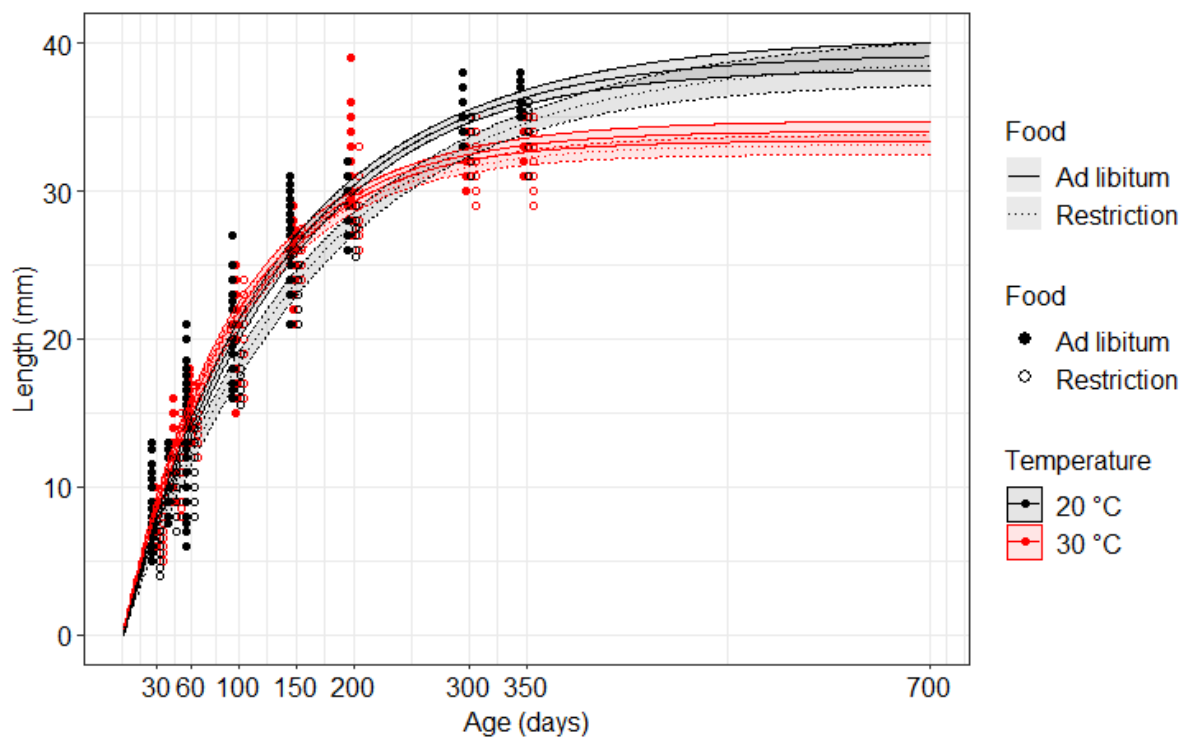
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The *cox.zph* function correlates the scaled Schoenfeld residuals with time for each covariate to test for independence between residuals and time. Additionally, it performs a global test for the model as a whole. From our model output, this test was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

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

BlueBlack and red colors represent the cold and warm treatments, respectively. Solid and dotted lines represent the ad libitum and the resourcefood restriction treatments, respectively. Areas represent the 95 % credibility intervals. Points represent experimentally measured sizes at age.