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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.

Introduction

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

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

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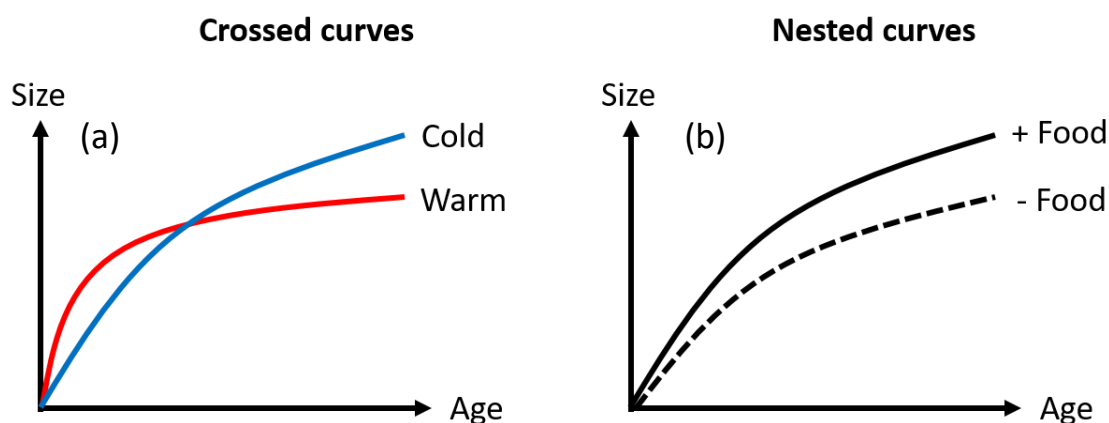
142   *Figure 1: Patterns of crossed vs. nested growth curves driven by (a) temperature and (b) food availability (after Berrigan*
143   *and Charnov 1994).*

144

Material and methods

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 F_0 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 F_0 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 F_1 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

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.

Statistical analysis

192

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

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

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 Bertallanfy 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    $$L_{\infty CT}\ N(0,0.001) \quad K_{CT}\ N(0,001) \quad t_{0CT}\ N(0,0.001) \quad \text{(eq. 2)}$$

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

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

210 With $\sigma_{L\infty}$, 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 $$L_{\infty t} = L_{\infty CT} + \varepsilon_{L_\infty t} \text{(eq. 4)}$$

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

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

220    $$L_{ftj}\ N\big(L_{tj}, \sigma\big)$$ $$\sigma\ U(0,10)$$ (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

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

## Results

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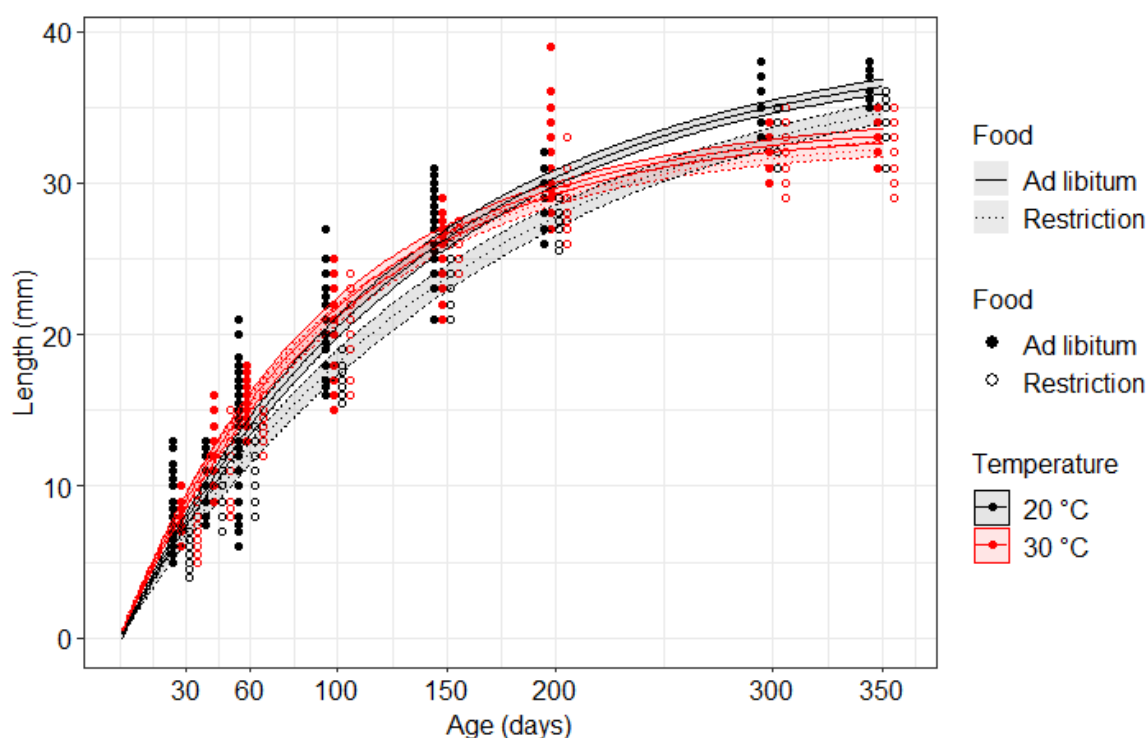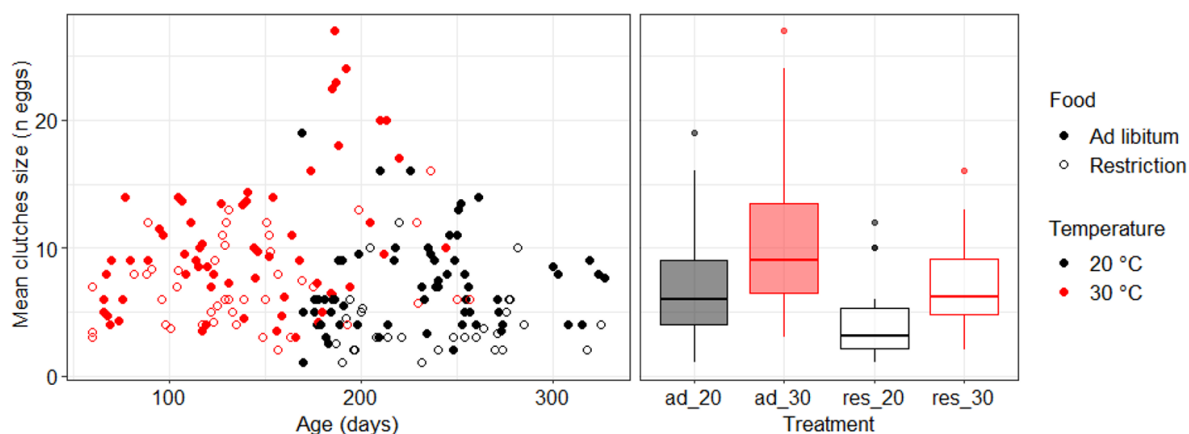

Figure 2: Fitted von Bertalanffy growth curve for each combination of temperature and food conditions.
Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively. Solid and dotted lines represent the ad libitum and the food restriction treatments, respectively. Areas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

258   In the warm treatment, the fish were sexually mature at 67.3 ± 2.3 days (body length: 16.8 ±
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

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.*

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).

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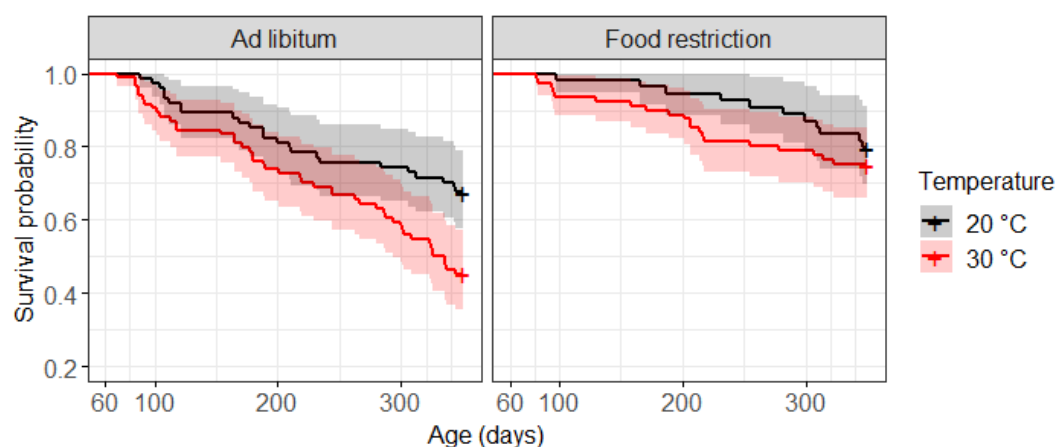
Figure 4: Kaplan-Meier survival curves for each combination of temperature and food conditions.
Black and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively. Solid and dashed lines
represent the ad libitum and the food restriction treatments, respectively. Shaded areas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

Discussion

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, locomotion, trophic interactions, or food web persistence and stability (Peters 1986, Calder 1996, Brown *et al.* 2004, Gibert and Delong, 2014, Sentis *et al.* 2017, Emmerson and Raffaelli 2004, Osmond *et al.* 2017, Lindmark *et al.* 2018). Shrinking body size with increasing temperature has been proposed as a third universal response to global warming (Daufresne *et al.* 2009, Gardner *et al.* 2011). In addition, the quantity and quality of resources are expected to change with global warming (De Senerpont Domis *et al.* 2014), in response to changes in physicochemical, phenological (Visser and Both, 2005) and geographical parameters (Parmesan and Yohe, 2003). The independent and interactive effects of temperature and food availability on life history traits have been mainly studied in small aquatic (Betini *et al.* 2020, Giebelhausen and Lampert 2001, Wojewodzic *et al.* 2011, Persson *et al.* 2011, Giberson and Rosenberg 1992) and terrestrial (Clissold and Simpson 2015, Corrêa *et al.* 2021, Stillwell *et al.* 2007, Rohner *et al.* 2017) invertebrate species. However, we have no 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 (Forster *et al.* 2012) and that body size reduction at higher trophic level can increase food web persistence at high temperature (Sentis *et al.* 2017). Our objective was thus to test whether food availability can modulate the effects of temperature on size at age and life history traits of a vertebrate predator species, the medaka fish.

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

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

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

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

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

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Data, scripts and codes availability

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

Conflict of interest disclosure

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686 ## Appendix

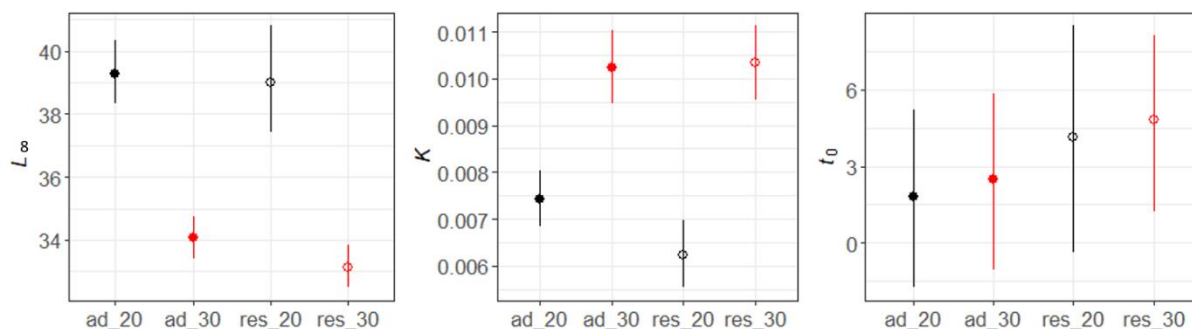687
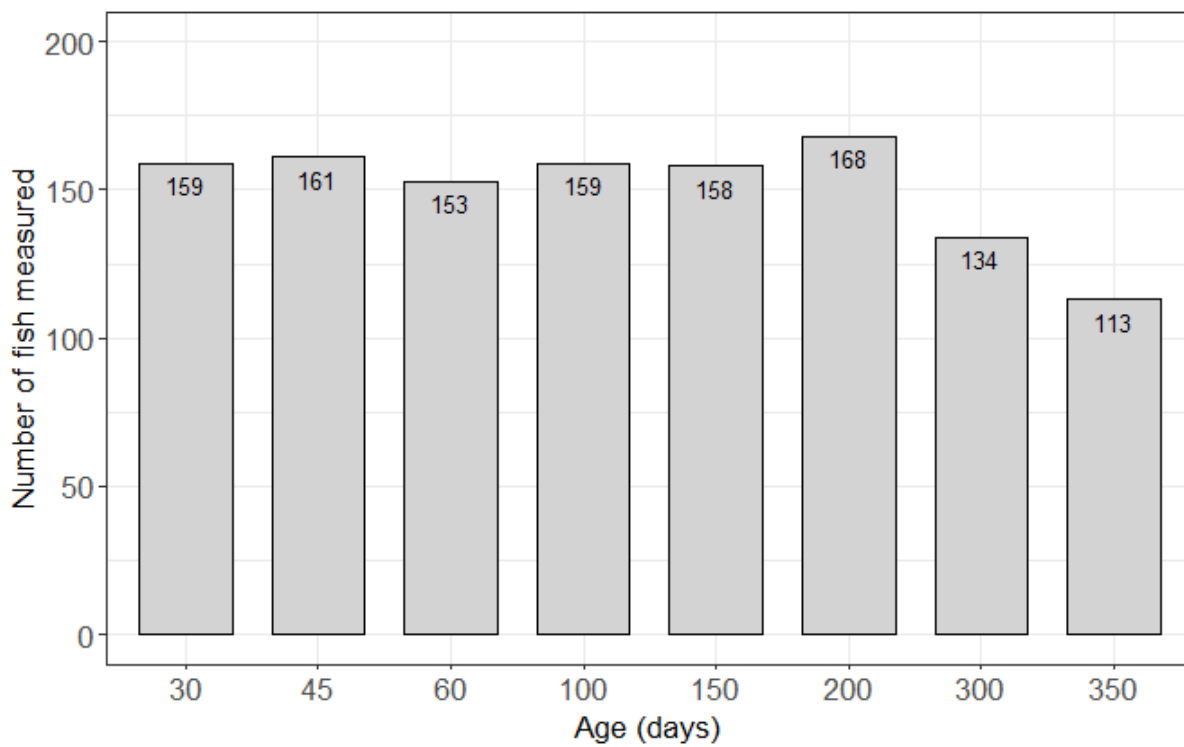
688

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

690

Fig. S 2 : Estimated Von Bertallanfy 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.

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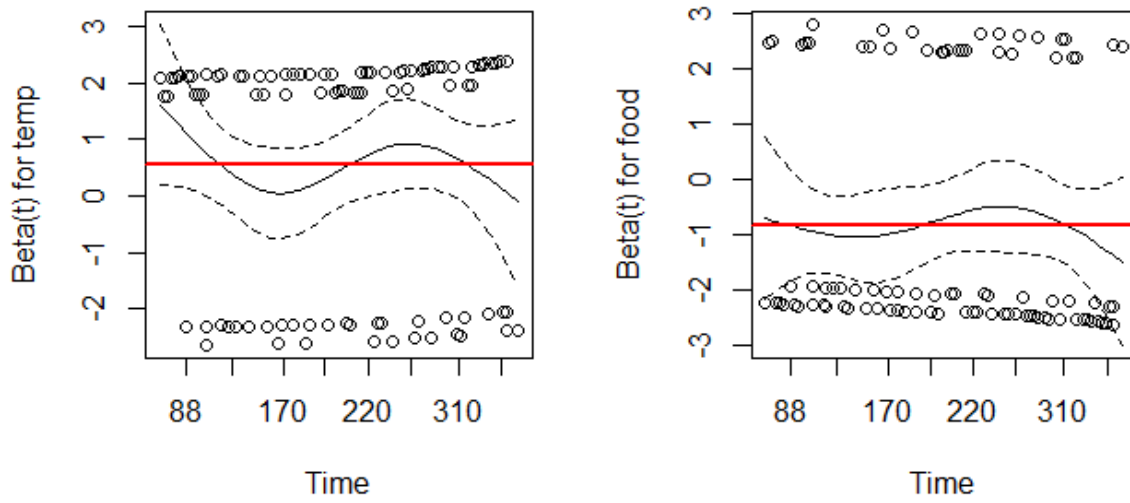
705 *Fig. S 3: Cox model assumption of proportionality for temperature and food condition.*

706   The *cox.zph* function correlates the scaled Schoenfeld residuals with time for each covariate to
707 test for independence between residuals and time. Additionally, it performs a global test for the model
708 as a whole. From our model output, this test was not statistically significant for temperature (*chi² =*
709 *0.20, df = 1, p = 0.65*), food (*chi² = 0.00, df = 1, p = 0.97*) and the global test (*chi² = 0.20, df = 2, p = 0.90*),
710 indicating a proportional hazards.

711

712
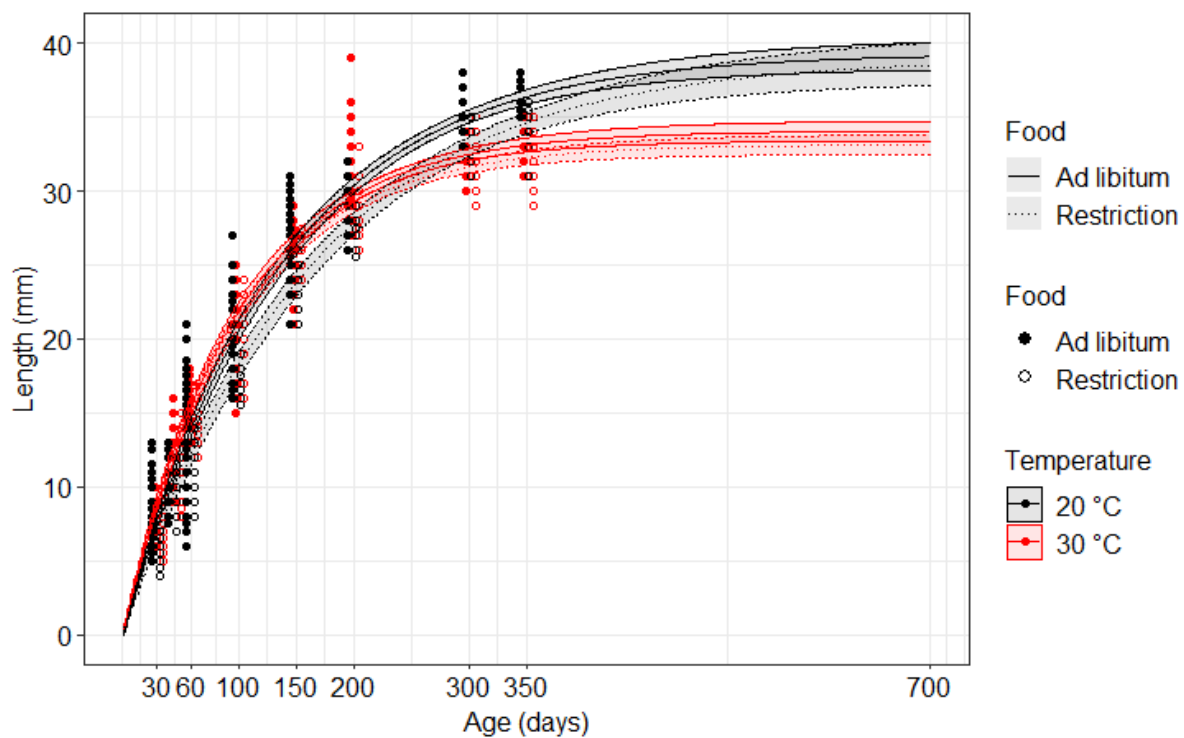
713 ***Fig. S 4: Extrapolation of Von Bertalanffy growth curve for each combination of temperature and food conditions.***
714 *Black and red colors represent the cold and warm treatments, respectively. Solid and dotted lines represent the ad libitum*
715 *and the food restriction treatments, respectively. Areas represent the 95 % credibility intervals.*
716 *Points represent experimentally measured sizes at age.*