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Distinct impacts of resource restriction and warming on growth and survival

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Abstract

The reduction of body size with warming has been proposed as the third universal response to global warming, besides geographical and phenological shifts. Observed body size shifts in ectotherms are mostly attributed to the temperature size rule (TSR) stating that warming speeds up initial growth rate but leads to smaller adult size when resource availability is not limiting growth. Nevertheless, climate warming can decrease resource availability by modifying biochemical cycles and primary production and it remains unclear if, and how, the TSR pattern holds under resource restriction. Resource availability can also influence growth and survival and thus potentially modulate the effect of temperature on the growth survival trade-off, although this remains untested. In this paper, we filled this gap by investigating under laboratory conditions the independent and interactive effects of temperature (20 or 30 °C) and resource availability (restricted or *ad libitum*) on the growth 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 fish were smaller than *ad libitum* fed fish throughout the experiment leading to nested growth curves. Resource 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 at 30 °C compared to 20 °C suggesting a "live fast die young" strategy where accelerated growth trades off with increased mortality. Resource restriction increased the survival probability under both temperature conditions corresponding to a "eat little die old" strategy when resource restriction decreases growth but increases longevity. Our results highlight the importance of accounting for the interaction between temperature and resource 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, resource restriction, temperature, TSR, growth, survival, trade-off, fish.

40 Introduction

41

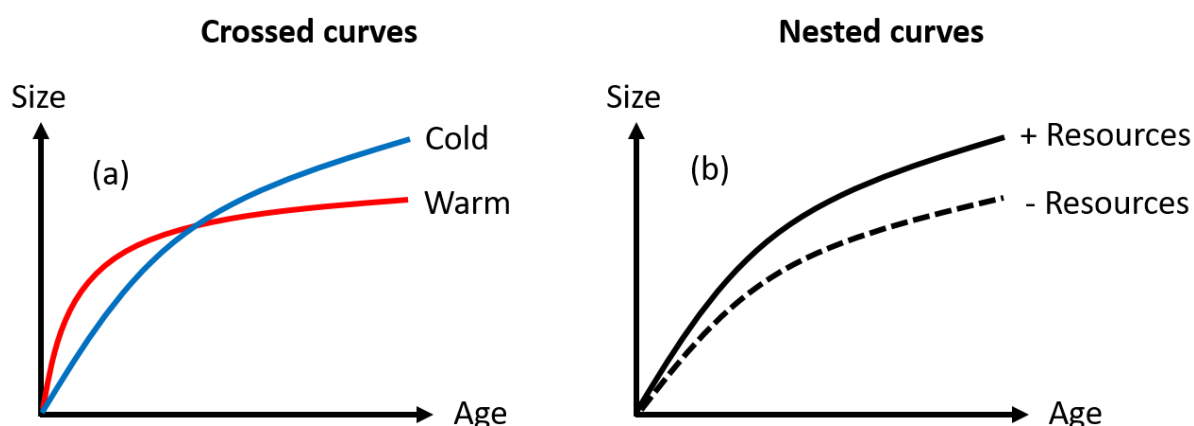
42 Body size reduction has been proposed as a third universal species response to global warming
43 (Daufresne *et al.* 2009, Gardner *et al.* 2011, Sheridan and Bickford 2011), in addition to changes in
44 phenology (Visser and Both 2005) and geographic distribution (Parmesan and Yohe 2003). While the
45 first two responses have been studied extensively (Meyer *et al.* 1999), the third one has received less
46 attention despite its high prevalence and magnitude. For instance, in aquatic ectotherms, body size
47 can reduce up to -8 % per °C (Forster *et al.* 2012). Previous studies focused mainly on proximal causes
48 of body size changes (Zuo *et al.* 2012, Atkinson and Sibly 1997) and their variability among species and
49 habitats (Horne *et al.* 2015, Forster *et al.* 2012, Atkinson 1994). At the individual level, body size shift
50 can be explained by the impact of temperature on the growth of ectotherms (Atkinson and Sibly 1997,
51 Berrigan and Charnov 1994, Perrin 1995, Arendt 2007, Arendt 2011). According to the "Temperature
52 Size Rule" (TSR), ectotherms grow faster but reach a smaller asymptotic size under warm environment
53 compared to colder ones, resulting in "crossed" growth curves (Figure 1). This pattern remains an
54 evolutionary puzzle (Atkinson and Sibly 1997) and could represent different growing and/or developing
55 strategies. For example, a recent study showed that warming accelerated growth and reproduction
56 leading to a rapid life cycle but also a decrease in adult survival in a temperate lizard species, a strategy
57 commonly referred to as "live fast die young" (Bestion *et al.* 2015).

58 Besides temperature, another major factor underlying growth and survival is resource
59 availability. Individuals need enough resources, as energy and material inputs, to sustain their
60 metabolic demand and optimize the allocation of energy to growth and reproduction (brown *et al.*
61 2004, Cross *et al.* 2015). Interestingly, resource restriction may also be beneficial to the lifespan of
62 organisms as this restriction reduces the production of senescence-accelerating oxidizing agents
63 during metabolism (Sohal and Weindruch 1996, Gredilla *et al.* 2001, Speakman 2005), resulting in a
64 "eat little die old" strategy. There is a long history of researches on the influence of resource availability
65 on the growth rate of ectothermic species (Rasmussen and Ostefeld 2000, Johnston *et al.* 2002). In
66 most cases, individuals with a higher resource availability have both a higher initial growth rate and a
67 larger asymptotic size compared to individuals under resource restriction. In contrast to the pattern of
68 crossed curves driven by temperature, different resource levels lead to a pattern of nested curves
69 where the growth curve under limiting resources is nested below the growth curve under unlimited
70 resources (Figure 1).

71 Phenological and geographical changes can alter the quantity and quality of resources in
72 predator-prey relationships by inducing temporal or spatial mismatches where the predator is left with
73 reduced resource availability (Boukal *et al.* 2019, Twining *et al.* 2022). For instance, in aquatic systems,
74 a temporal shift in the spring bloom of diatoms explained the long-term decline of a daphnia
75 population in a large temperate lake because of a temporal mismatch between the diatom bloom and
76 the beginning of the growing season for the daphnia population (Winder and Schindler 2004). These
77 phenological asynchronies can alter the structure and dynamics of food webs and modify ecosystem
78 processes (Damien and Tougeron 2019). Moreover, warming can also decrease resource quality by
79 benefiting small phytoplankton taxa of low nutritional quality such as picocyanobacteria or
80 filamentous bacteria (Paerl and Huisman 2008, Paerl 2014, Ekvall *et al.* 2013, Urrutia-Cordero *et al.*
81 2017).

82 Although the effects of food availability and temperature have been extensively studied
 83 independently, the interactive effects of these two factors remain relatively unknown. Only a few
 84 studies have shown that resource quantity (Betini *et al.* 2020, McLeod *et al.* 2013) and quality
 85 (Wojewodzic *et al.* 2011, Persson *et al.* 2011) can modulate the temperature effect on growth rates
 86 and survival in daphnia and fish. This is an important gap because, as explained above, temperature
 87 and resource availability can covary. We thus need to account for both the direct physiological impact
 88 of temperature as well as its indirect effects through modified resource availability to better understand
 89 the impacts of climate change on the growth-survival trade-off.

90 In this study, we address this gap by experimentally investigating growth and survival of a small
 91 Japanese fish, the medaka (*Oryzias latipes*, Temminck & Schlegel), raised at two temperatures (20 and
 92 30 °C) with and without resource restriction. Our objective was to test whether resource restriction
 93 can modulate the effects of temperature on the growth and survival pattern of an ectotherm species.
 94 We discuss the implication of our findings on (i) the importance of accounting for the temperature-
 95 resource interaction in the context of global warming, as the quantity and nutritional quality of
 96 phytoplankton and zooplankton are modified by global warming (De Senerpont Domis *et al.* 2014) and
 97 (ii) to which extent investigating growth and survival patterns could help disentangling the relative
 98 impacts of temperature and resources availability on body size shifts under global warming.



99
 100 **Figure 1: Patterns of crossed vs. nested growth curves driven by (a) temperature and (b) resource availability (after**
 101 **Berrigan and Charnov 1994).**

102

103 Material and methods

104 Biological system and rearing conditions

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106

107 The medaka is a small iteroparous freshwater fish native to East Asia (Hirshfield 1980). The life
 108 span of a medaka is about 2 years and its adult size varies between 30 and 50 mm (Ding *et al.* 2010,
 109 Egami and Etoh, 1969). This is an eurythermal species (5 °C - 35 °C) with an optimum temperature of
 110 25 °C (Dhillon and Fox 2004). At this temperature, the medaka requires only 10 to 12 weeks to reach
 111 sexual maturity. Fish were maintained in the laboratory using an open water system with water supply
 112 controlled by drip emitters (1 L.h⁻¹). Input water quality was maintained with mechanical, biological
 113 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.

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

123 From this F₀ generation, about 300 eggs were collected in each tank. Eggs were placed in small
 124 nurseries (2.5 L) made of fine mesh and each nursery was placed in the tank where the eggs were
 125 collected from (see Hemmer-Brepson *et al.* 2014, Loisel *et al.* 2019 for more details). After 30 days of
 126 growth, the parents were removed and the F₁ fish larvae were reared under four different treatment:
 127 ad_20 (*ad libitum* and 20 °C), res_20 (restriction and 20 °C), ad_30 (*ad libitum* and 30 °C) and res_30
 128 (restriction and 30 °C). For each treatment, the growth of approximately 80 fish was monitored, except
 129 for res_20 where only 54 fish could be maintained. Fish were maintained in 20 L aquaria with 20 - 30
 130 fish of a single treatment. This density (less than 2 - 3 fish per liter) does not cause any stress or
 131 agonistic behaviour in this species (Denny *et al.* 1991). The fish were fed with TetraMin[®] (composition:
 132 47 % protein, 10 % fat content, 3 % cellulose and 6 % water) every morning (for the *ad libitum*
 133 condition) or every two mornings (for the restriction condition). On each feeding days, TetraMin[®] was
 134 provided to each tank until the fish no longer went up to the surface to get food. Excess food was
 135 systematically removed after feeding to prevent feeding between two meals. Apart from temperature
 136 and resource, all the experimental parameters were similar in the four treatments.

137 Growth measurement and survival

138
 139 The total length (from the head to the tip of the caudal fin, TL) of each fish was measured with
 140 a precision of 0.5 mm at 30, 45, 60, 100, 150, 200, 300 and 350 days. Fish were measured after placing
 141 them on a 5 cm diameter Petri dish layered with a millimeter graph paper and filled with water. They
 142 were then immediately released into their respective tank. An average of 150.6 ± 18.1 fish were
 143 measured per age (see Fig. S 1 for more details). As fish were not identify individually, the growth
 144 curves applies to the experimental population (i.e. one curve per treatment) and not to individuals.
 145 Survival was monitored daily from 65 days (age of first sexually mature fish) until the end of the
 146 experiment.

147 Statistical analysis

148
 149 TL measurements and ages were used to fit von Bertalanffy growth curve model (Von
 150 Bertalanffy 1938):

$$151 \quad L_t = L_\infty(1 - e^{-k(t-t_0)}) \quad (\text{eq. 1})$$

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

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

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

166 We then used (eq. 1) to estimate the expected mean total length L_j for each fish (j), depending of its
 167 age (t_j) and its temperature and resource condition:

$$168 \quad L_j = L_{\infty CT} \left(1 - e^{-k_{CT}(t_j - t_{0C})} \right) \quad (\text{eq. 3})$$

169 Finally, we hypothesized that the observed total length of each fish, L_t , was normally distributed:

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

171 To compare the growth patterns among temperature and resource conditions, we plotted the average
 172 growth curves (eq. 3) and their credible interval (CI) using the posterior distributions of the parameters
 173 (L_∞ , K , t_0) that were obtained from five independent Monte-Carlo Markov Chains (see Fig. S 2 for more
 174 details on the estimated parameter values). For each chain, after an initial burning of 50 000 values,
 175 200 000 iterations were computed and we conserved one value every 100 iterations to limit
 176 autocorrelation between estimations. The posterior distributions for each average total length at age
 177 (L) were thus constituted of 10,000 values. The quantiles 2.5 % and 97.5 % were used to estimate
 178 credibility intervals CIs. We compared the growth curves among our four experimental treatments by
 179 investigating the overlap among their CIs. Curves were considered as significantly different when their
 180 CIs do not overlap (Pritchard *et al.* 2017).

181 We investigated the effects of temperature, resource restriction and their interaction on
 182 survival probability using a Cox proportional hazards model (*coxph* function in the "survival" package
 183 (Therneau *et al.* 2022)) followed by a variance analysis *anova*. We tested the Cox model proportional
 184 hazards assumption using the Global test statistic from the *cox.zph* function (see Fig. S 3 for more
 185 details).

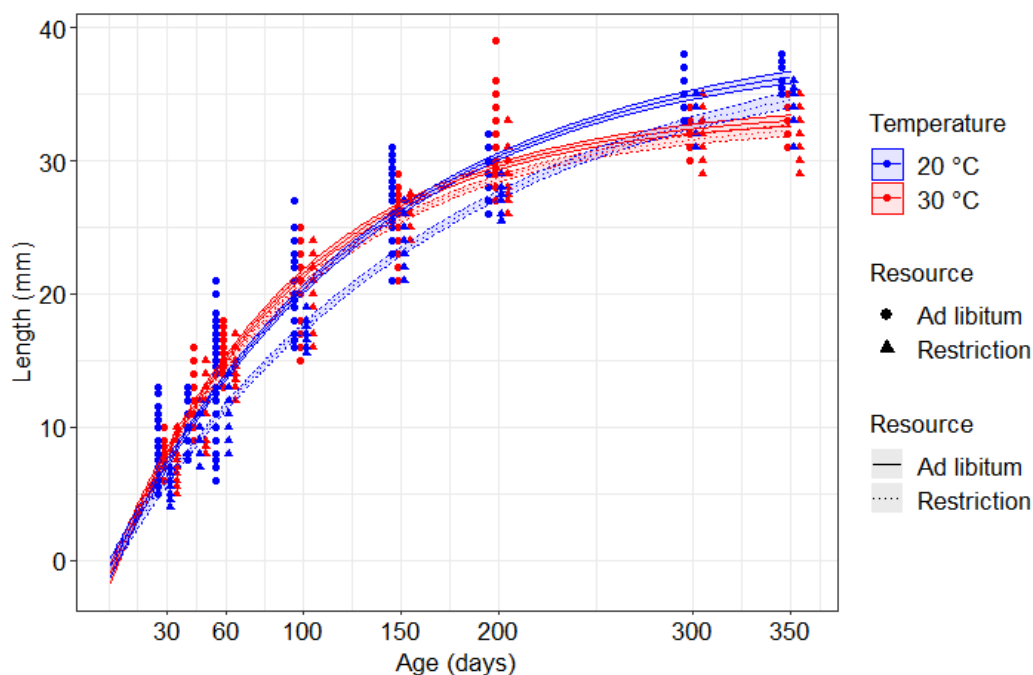
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187 Results

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189 We found that, at both resource conditions, warming leads to crossed growth curves by
 190 increasing initial growth rate and decreasing adult size, although the curves crossed later for the
 191 resource-restricted fish (Figure 2). Resource restriction in the cold treatment leads to nested
 192 growth curves throughout the experiment by decreasing the initial growth rate and adult size. Growth curves
 193 are also nested over almost the entire experiment in the warm treatment (Figure 2).

194

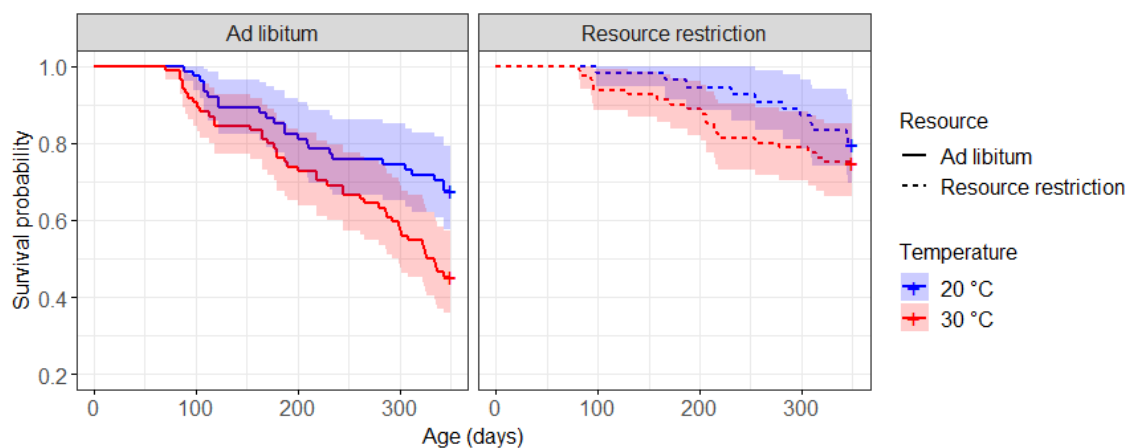


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196 **Figure 2: Fitted von Bertalanffy growth curve for each combination of temperature and resource conditions.**
 197 Blue and red colors represent the cold and warm treatments (i.e. 20 and 30 °C), respectively. Solid and dotted lines represent
 198 the ad libitum and the resource restriction treatments, respectively. Areas represent the 95 % credibility intervals.
 199 Jittered points represent experimentally measured sizes (in mm) at age (in days).

200

201 The fish survival probability was not significantly affected by the interaction between warming
 202 and resource restriction ($\chi^2 = 0.69$, $df = 1$, $p = 0.41$, $n = 292$). In contrast, warming significantly reduced
 203 the fish survival probability ($\chi^2 = 7.29$, $df = 1$, $p = 0.01$, $n = 292$). Moreover, resource restriction
 204 significantly increased survival probability ($\chi^2 = 16.34$, $df = 1$, $p < 0.001$, $n = 292$) (Figure 3).



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Figure 3: Kaplan-Meier survival curves for each combination of temperature and resource conditions. Blue 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 resource restriction treatments, respectively. Shaded areas around the lines represent the 95 % confident intervals.

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211 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, 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). Although the effects of temperature and resource on growth and survival have been largely studied independently (Daufresne *et al.* 2009, Forster *et al.* 2012, Rasmussen and Ostefeld 2000, Johnston *et al.* 2002), the interactive effects of these two factors on the growth-survival trade-off remain relatively unknown, despite its potential implications for community dynamics and interspecific interactions (Werner and Anholt 1993). Our objective was thus to test whether resource availability can modulate the effects of temperature on the size at age growth and survival pattern of a common fish used in labs, the medaka.

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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

237 energetic demands of organisms, and thus also alters the strength of trophic interactions. For example,
238 higher temperature has been shown to increase short-term predator-prey interaction strength and
239 predator energetic efficiency (Sentis *et al.* 2012). These different studies illustrate the importance of
240 considering size and temperature in studies of global warming effects. To date, studies examining the
241 consequences of temperature-induced body size shifts on trophic interactions, community dynamics,
242 and food web structure, only considered the reduction in adult size (Sentis *et al.* 2017, Osmond *et al.*
243 2017, Lindmark *et al.* 2018). However, warming leads to larger juvenile but smaller adults and thus the
244 impacts of temperature-induced body size shifts on ecosystem functioning certainly depends on life
245 stages.

246 Furthermore, size and temperature alter the metabolism and energy requirements of
247 organisms (Brown *et al.* 2004) which implies that resource also plays a crucial role in the overall
248 responses of aquatic ecosystems to climate warming (Ruiz *et al.* 2020). In our study, despite the curves
249 being nested throughout the experiment at both temperatures in agreement with previous studies
250 (Rasmussen and Ostefeld 2000, Johnston *et al.* 2002), the resource restriction effects appeared to be
251 greater at 20 °C where the curves were more nested than at 30 °C. This is surprising because we
252 expected resource restriction to have more effect at 30 °C as warming increases metabolic rates which
253 implies higher energy demand and feeding rate to sustain high metabolic costs (Brown *et al.* 2004).
254 Our result is in line with recent studies investigating the interactive effects of temperature and
255 resource availability on aquatic organisms such as daphnia (Wojewodzic *et al.* 2011, Persson *et al.*
256 2011, Betini *et al.* 2020) and fish (McLeod *et al.* 2013). For example, Betini *et al.* 2020 showed that the
257 reduction in body size induced by temperature was greater under low resources conditions. Similar
258 results were observed in *Amphiprion percula* larvae, where low resource availability limited growth
259 rates in warm condition (McLeod *et al.* 2013). Wojewodzic *et al.* (2011) and Persson *et al.* (2011)
260 reported that somatic growth rates of daphnia decrease as C:P ratios in resources increase, and that
261 this effect is amplified under warming. These results suggest that temperature-induced body size shifts
262 depend on the quantity but also the quality of resources (Wojewodzic *et al.* 2011, Persson *et al.* 2011).
263 In addition, the survival probability of fish in our experiment was influenced by both temperature and
264 resource restriction. Indeed, fish reared at 30 °C had a lower survival probability than fish reared at 20
265 °C while resource restriction increased the survival probability under both temperature conditions.
266 This beneficial effect of resource restriction on survival probability was also observed in frog larvae
267 (Courtney Jones *et al.* 2015) and daphnia (Betini *et al.* 2020). Lower resource availability implies a
268 decrease in metabolism and thus a lower production of oxidizing agents which contributes to slow
269 down senescence and increase survival probability after maturity, resulting in a "eat little die old"
270 strategy (Sohal and Weindruch, 1996, Gredilla *et al.* 2001, Speakman 2005, Pifferi *et al.* 2018). Our
271 results potentially illustrates different developmental strategies. For example, at 30 °C, fish may have
272 maintained a high growth rate despite resource restriction in order to maintain a rapid life cycle, at
273 the expense of lower survival. This hypothesis is supported by the fact that mortality was higher and
274 sexual maturity was reached at a younger age (65 days at 30 °C against 160 days at 20 °C, unpublished
275 data) and smaller size (17 mm at 30 °C against 26.5 mm at 20 °C, unpublished data) at 30 °C. This
276 strategy is commonly referred to as "live fast die young strategy" (Bestion *et al.* 2015). Ultimately,
277 measuring the fitness of the fish under the different conditions would help understanding if these two
278 strategies (i.e. eat little die old and live fast die young) are adaptive or results from physiological
279 constraints than are difficulty overpassed by evolutionary adaptations.

280 Resource-restricted fish were smaller than *ad libitum* fed fish. Thus, in our study, resource
281 restriction appears to amplify TSR by decreasing initial growth rate and adult size in the cold and warm
282 treatments, respectively. Cross *et al.* (2015) suggested that the warming effects on growth could be
283 amplified by low resource availability, particularly in single-celled organisms such as algae and bacteria,
284 because small cells tend to have lower nutritional requirements and increased nutrient acquisition
285 compared to large cells (Cross *et al.* 2015). A recent study tested this hypothesis by investigating the
286 warming effects on protist growth under the influence of different resource availability and
287 interspecific competition (Tan *et al.* 2021). The warming effects on body size were not exacerbated by
288 low resource availability or high interspecific competition. Instead, the authors found that interspecific
289 competition elongates the body shape of protists, increasing their swimming speed and resource
290 acquisition ability, potentially making up for low resource availability (Tan *et al.* 2021). Another recent
291 study also indicates that organism's evolutionary responses to warming can mitigate resource
292 restrictions, thereby avoiding constraints on whole-organism growth (Verberk *et al.* 2020). For
293 example, organisms can increase the surface area for resource uptake by altering body shape,
294 increasing organ surface area, or modulating feeding activity or locomotion (Verberk *et al.* 2020).
295 Although our results suggest that TSR was amplified by resource restriction, the effects of resource
296 restriction were relatively weak. This may therefore be explained by potential acclimation of medaka
297 to rearing temperatures or by a resource restriction not severe enough. The resource provided to the
298 fish was not weighed for convenience and logistic limitations. Reducing feeding events by half (1 out
299 of 2 mornings) was considered restrictive and significantly affected survival. However, resource
300 restriction did not appear to be strong enough to observe a significant effect on adult fish size at 30
301 °C. Resource effects would likely have been more pronounced if restriction had been greater.

302 Overall, we found that temperature significantly increased initial growth rate and decreased
303 adult size leading to crossed growth curves, consistent with TSR. Resource restriction led to nested
304 growth curves, but the effects appeared to be greater at 20 °C. Resource restriction thus appears to
305 amplify TSR by decreasing initial growth rate and adult size in the cold and warm treatments,
306 respectively. To our knowledge, this is the first experiment showing that resource restriction amplified
307 TSR in fish. The results of this experiment demonstrate the importance of considering the interactions
308 between temperature, body size and resource. Moreover, we found a trade-off between growth and
309 survival with accelerated growth but lower survival under warming. Resource restriction modulated
310 this trade-off by decreasing growth and increasing survival. Under warming, we may thus expect
311 species to live faster but die younger unless resource becomes limiting. As a consequence, the final
312 outcome will depend on how temperature changes relative to resource availability. The interacting
313 effect of resource and temperature on body size has also been demonstrated at larger scales and in
314 particular for trophic interaction strength, food chain persistence, and food web stability (Sentis *et al.*
315 2014, Binzer *et al.* 2012, Binzer *et al.* 2016). Our results suggest that accounting for life history trade-
316 offs could be important to better understand the effect of global change on these different levels of
317 complexity. Furthermore, only body size reduction was considered in recent studies (Sentis *et al.* 2017,
318 Osmond *et al.* 2017, Lindmark *et al.* 2018) while juveniles are larger under warming. We emphasize
319 the importance of proceeding investigations by considering ontogeny in future studies since the
320 temperature effect on growth are dependent on life stages. We suggest that bioenergetic models such
321 as the Dynamic Energy Budget (DEB) or Metabolic Theory of Ecology (MTE) could be powerful to study
322 the temperature-size-resource relationships on individual growth (Zuo *et al.* 2012) and survival.
323 Indeed, these models can quantify the incoming and outgoing flows of matter and energy while

324 complying to the fundamental laws of thermodynamics (Kooijman 2000). It would thus be possible to
 325 investigate temperature and nutritional quantity and/or quality to study their independent and
 326 interactive effects on energy allocation to maintenance, growth or survival. Bioenergetics models
 327 coupled with population dynamics models, such as in Sentis *et al.* (2020), show promise for studying
 328 how trade-offs at the individual level impact trophic interactions, food webs and ecosystem processes
 329 under global change.

330

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 333 fish rearing.

334 Data, scripts and codes availability

335 Data, scripts and code are available online : <https://doi.org/10.6084/m9.figshare.20375850.v1>

336 Conflict of interest disclosure

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

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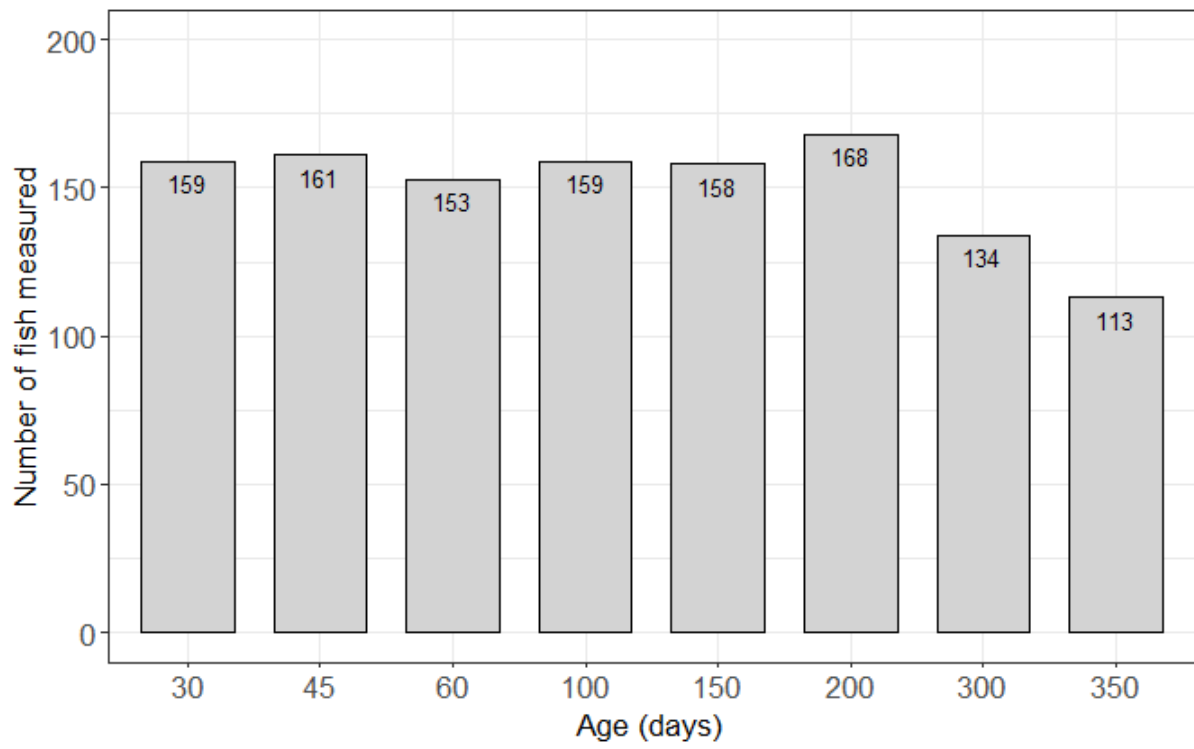
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540 Appendix

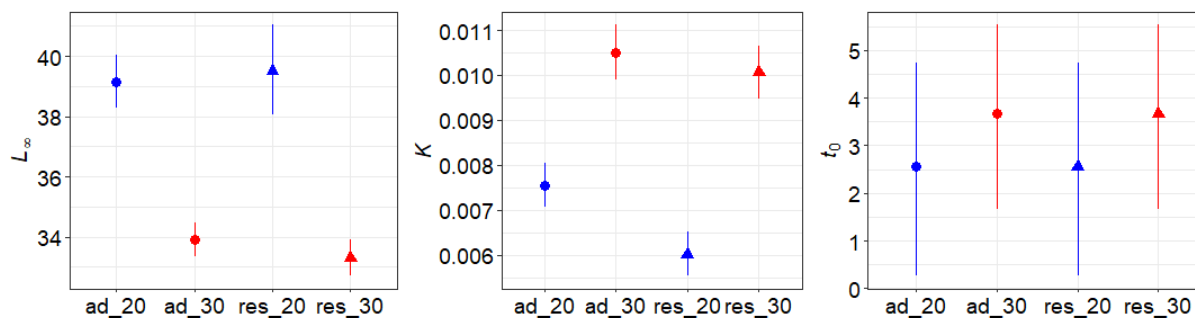
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Fig. S 1: Number of fish measured at different ages.



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

Blue and red colors correspond to the cold and warm treatments, respectively. Circles and triangles correspond to the *ad libitum* and resource restriction treatments, respectively. Bars represent 95 % credibility intervals.

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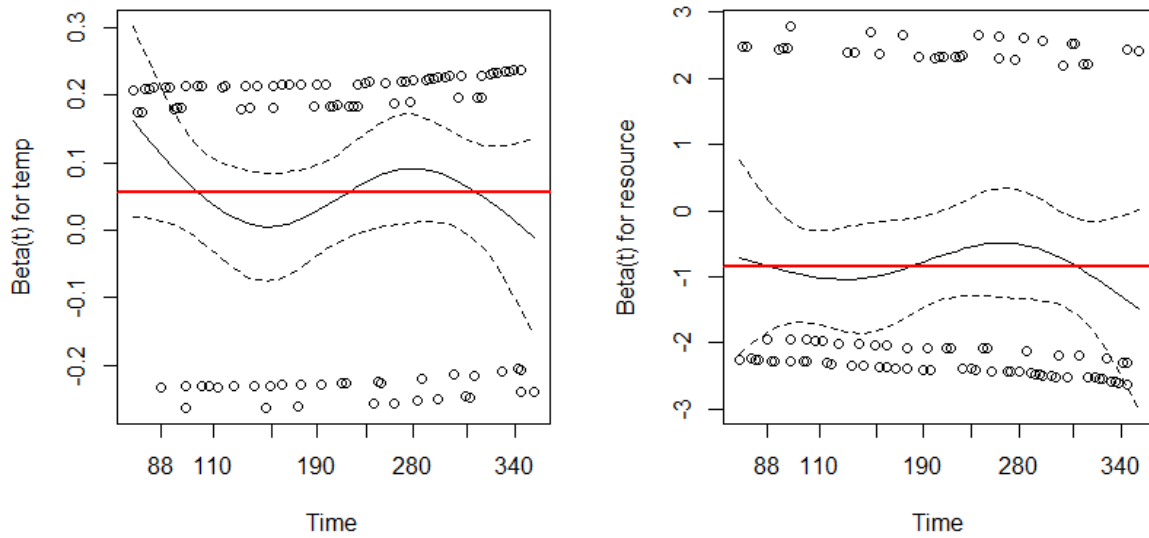
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Consistent with the experimental curves and TSR, warming significantly increased the initial growth rate K and decreased the maximum asymptotic size L_{∞} . Resource restriction had no effect on the initial growth rate K for fish reared at 30 °C, but significantly reduced K for fish reared at 20 °C. At the end of our experiment, the adult size of resource restricted fish was smaller than that of *ad libitum* fed fish, especially at 20 °C. Yet, resource 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 resource 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 320 days under cold and warm conditions, respectively (Fig. S 4). The theoretical age at which body size is zero t_0 was not significantly different between temperature conditions.



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

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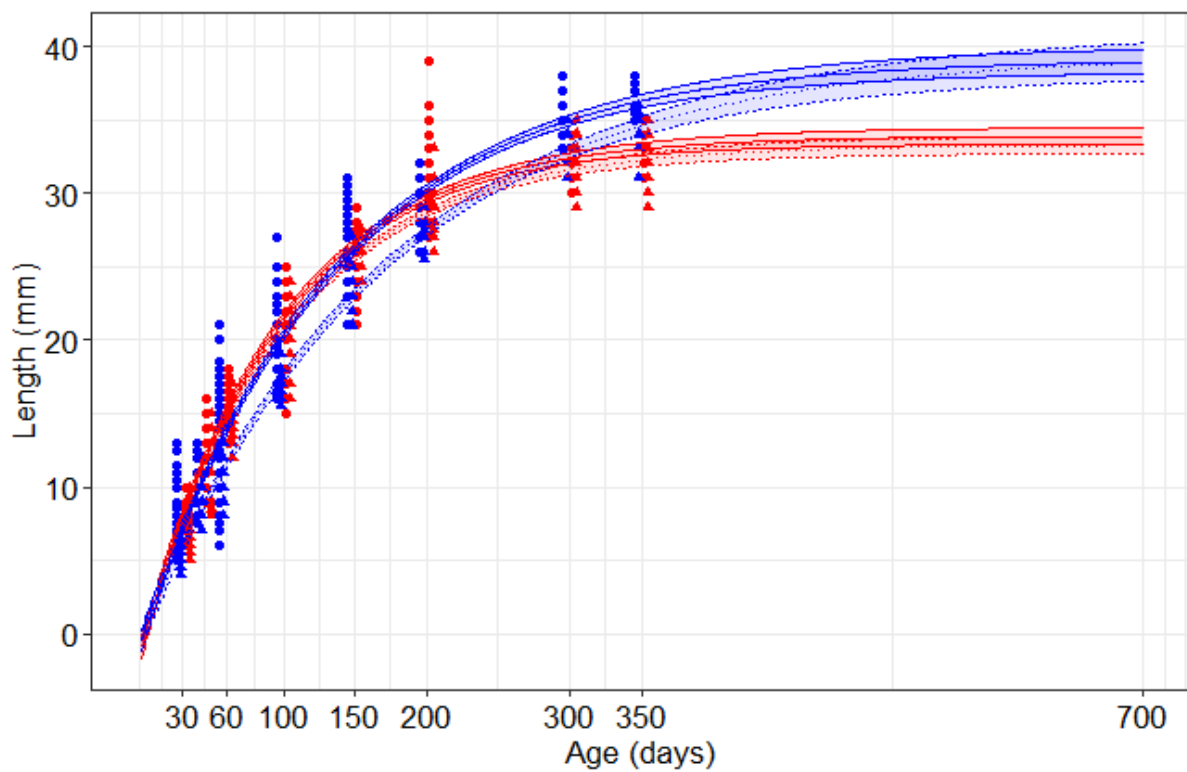
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The *cox.zph* function correlates the scaled Schoenfeld residuals with time for each covariate to test for independence between residuals and time. Additionally, it performs a global test for the model as a whole. From our model output, this test was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

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567 **Fig. S 4: Extrapolation of Von Bertalanffy growth curve for each combination of temperature and resource conditions.**
 568 Blue and red colors represent the cold and warm treatments, respectively. Solid and dotted lines represent the ad libitum
 569 and the resource restriction treatments, respectively. Areas represent the 95 % credibility intervals.
 570 Points represent experimentally measured sizes at age.