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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.

## Introduction

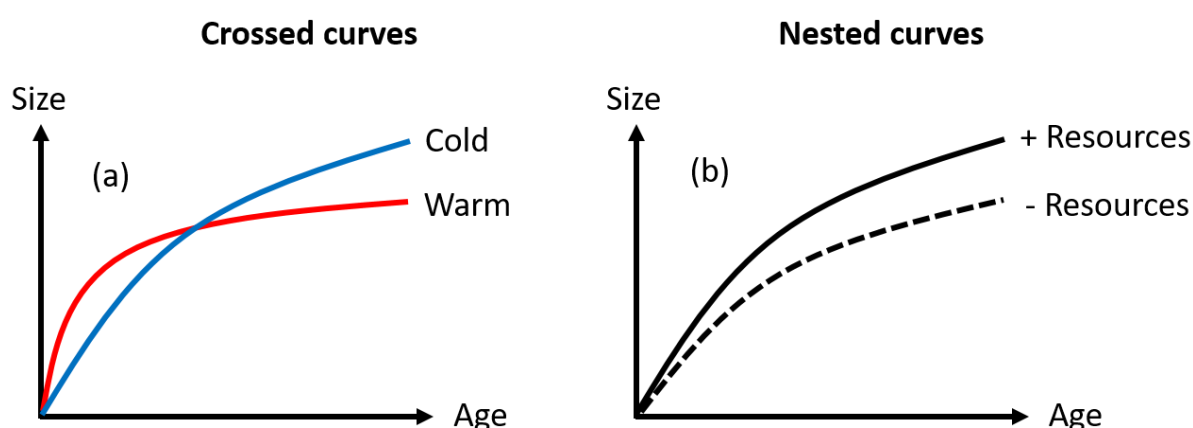
Body size reduction has been proposed as a third universal species response to global warming (Daufresne *et al.* 2009, Gardner *et al.* 2011, Sheridan and Bickford 2011), in addition to changes in phenology (Visser and Both 2005) and geographic distribution (Parmesan and Yohe 2003). While the first 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, in aquatic ectotherms, body size can reduce up to -8 % per °C (Forster *et al.* 2012). Previous studies focused mainly on proximal causes of body size changes (Zuo *et al.* 2012, Atkinson and Sibly 1997) and their variability among species and habitats (Horne *et al.* 2015, Forster *et al.* 2012, Atkinson 1994). 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). According to the "Temperature Size Rule" (TSR), ectotherms grow faster but reach a smaller asymptotic size under warm environment compared to colder ones, resulting in "crossed" growth curves (Figure 1). This pattern 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 accelerated 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).

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

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

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

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



**Figure 1: Patterns of crossed vs. nested growth curves driven by (a) temperature and (b) resource 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 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 supply controlled by drip emitters (1 L.h<sup>-1</sup>). 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  $F_0$  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  $F_0$  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  $F_1$  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, except for res\_20 where only 54 fish could be maintained. Fish were maintained in 20 L aquaria with 20 - 30 fish of a single treatment. This density (less than 2 - 3 fish per liter) does not cause any stress or agonistic behaviour in this species (Denny *et al.* 1991). The fish were fed with TetraMin® (composition: 47 % protein, 10 % fat content, 3 % cellulose and 6 % water) every morning (for the *ad libitum* condition) or every two mornings (for the restriction condition). On each feeding days, TetraMin® was provided to each tank until the fish no longer went up to the surface to get food. Excess food was systematically removed after feeding to prevent feeding between two meals. Apart from temperature and resource, all the experimental parameters were similar in the four treatments.

## Growth measurement and survival

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

## Statistical analysis

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

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

Where  $L_t$  is the estimated total length at time  $t$ ,  $L_{\infty}$  the maximum asymptotic size (i.e. the total length for fish with an  $\infty$  age),  $K$  the initial growth rate, and  $t_0$  the theoretical age at which body size is null.

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

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

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

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

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

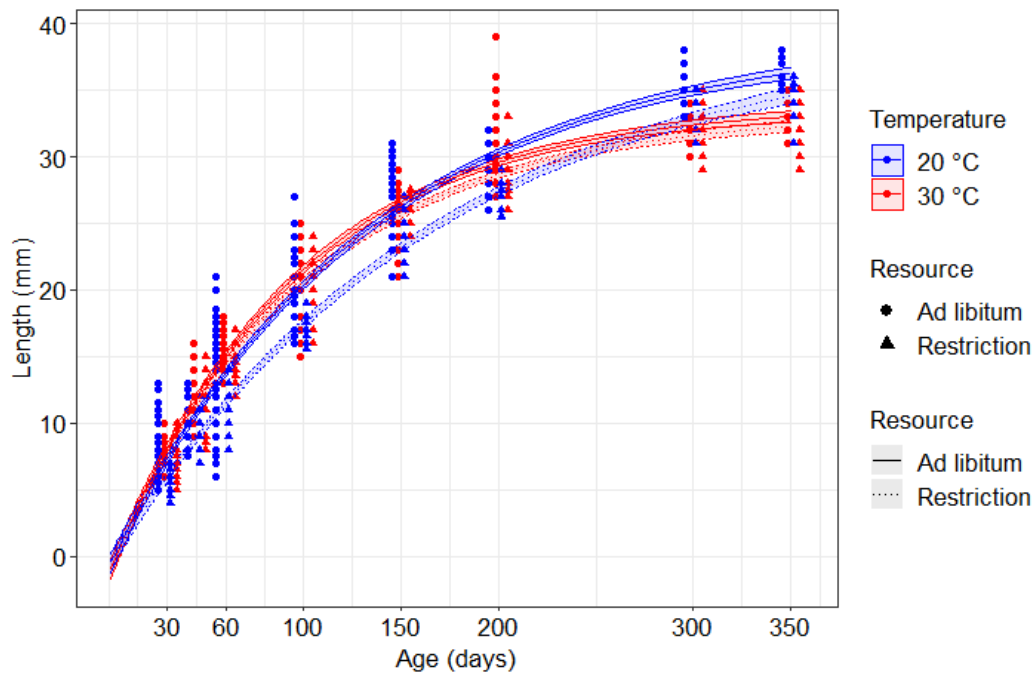
$$\begin{aligned} & L_{tj} \sim N(L_j, \sigma) \\ & \sigma = \frac{1}{\sqrt{\tau_{L_{tj}}}} & & \text{(eq. 4)} \\ & \tau_{L_{tj}} \sim \Gamma(0.001, 0.001) \end{aligned}$$

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

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

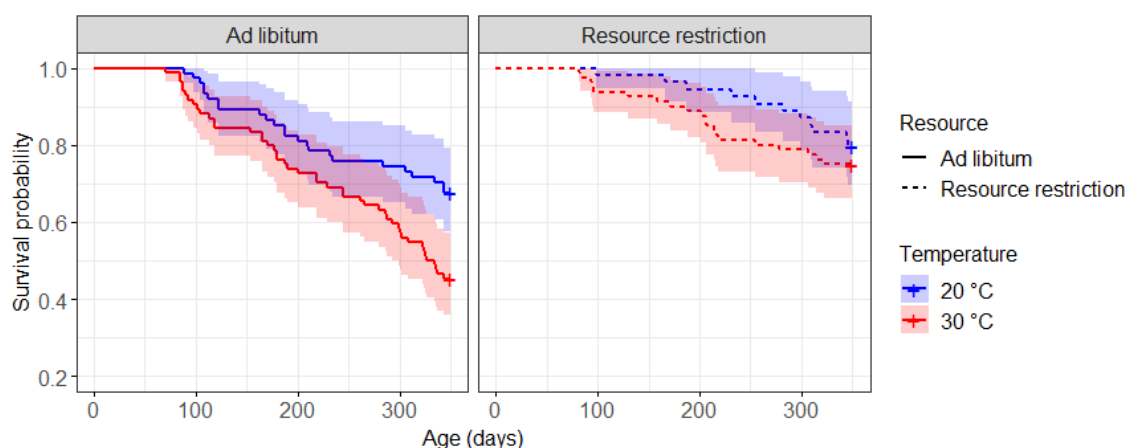
## Results

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



**Figure 2: Fitted von Bertalanffy growth curve 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 dotted lines represent the ad libitum and the resource restriction treatments, respectively. Areas represent the 95 % credibility intervals. Jittered points represent experimentally measured sizes (in mm) at age (in days).

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



**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.

## 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). 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 Ostensfeld 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.

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, warming leads to larger juvenile but smaller adults and thus the impacts of temperature-induced body size shifts on ecosystem functioning certainly depends on life stages.

Furthermore, size and temperature alter the metabolism and energy requirements of organisms (Brown *et al.* 2004) which implies that resource also plays a crucial role in the overall responses of aquatic ecosystems to climate warming (Ruiz *et al.* 2020). In our study, despite the curves being nested throughout the experiment at both temperatures in agreement with previous studies (Rasmussen and Ostensfeld 2000, Johnston *et al.* 2002), the resource restriction effects appeared to be greater at 20 °C where the curves were more nested than at 30 °C. This is surprising because we expected resource restriction to have more effect at 30 °C as warming increases metabolic rates which implies higher energy demand and feeding rate to sustain high metabolic costs (Brown *et al.* 2004). Our result is in line with recent studies investigating the interactive effects of temperature and resource availability on aquatic organisms such as daphnia (Wojewodzic *et al.* 2011, Persson *et al.* 2011, Betini *et al.* 2020) and fish (McLeod *et al.* 2013). For example, Betini *et al.* 2020 showed that the reduction in body size induced by temperature was greater under low resources conditions. Similar results were observed in *Amphiprion percula* larvae, where low resource availability limited growth rates in warm condition (McLeod *et al.* 2013). Wojewodzic *et al.* (2011) and Persson *et al.* (2011) reported that somatic growth rates of daphnia decrease as C:P ratios in resources increase, and that this effect is amplified under warming. These results suggest that temperature-induced body size shifts depend on the quantity but also the quality of resources (Wojewodzic *et al.* 2011, Persson *et al.* 2011). In addition, the survival probability of fish in our experiment was influenced by both temperature and resource restriction. Indeed, fish reared at 30 °C had a lower survival probability than fish reared at 20 °C while resource restriction increased the survival probability under both temperature conditions. This beneficial effect of resource restriction on survival probability was also observed in frog larvae (Courtney Jones *et al.* 2015) and daphnia (Betini *et al.* 2020). Lower resource availability implies a decrease in metabolism and thus a lower production of oxidizing agents which contributes to slow down senescence 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 illustrate different developmental strategies. For example, at 30 °C, fish may have maintained a high growth rate despite resource 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 (65 days at 30 °C against 160 days at 20 °C, unpublished data) and smaller size (17 mm at 30 °C against 26.5 mm at 20 °C, unpublished data) at 30 °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 difficultly overpassed by evolutionary adaptations.

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

Overall, we found that temperature significantly increased initial growth rate and decreased adult size leading to crossed growth curves, consistent with TSR. Resource restriction led to nested growth curves, but the effects appeared to be greater at 20 °C. Resource restriction thus appears to amplify TSR by decreasing initial growth rate and adult size in the cold and warm treatments, respectively. To our knowledge, this is the first experiment showing that resource restriction amplified TSR in fish. The results of this experiment demonstrate the importance of considering the interactions between temperature, body size and resource. Moreover, we found a trade-off between growth and survival with accelerated growth but lower survival under warming. Resource restriction modulated this trade-off by decreasing growth and increasing survival. Under warming, we may thus expect species to live faster but die younger unless resource becomes limiting. As a consequence, the final outcome will depend on how temperature changes relative to resource availability. The interacting effect of resource 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 reduction was 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 since the temperature effect on growth is dependent on life stages. 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-resource 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.* (2020), 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.v1>

## Conflict of interest disclosure

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

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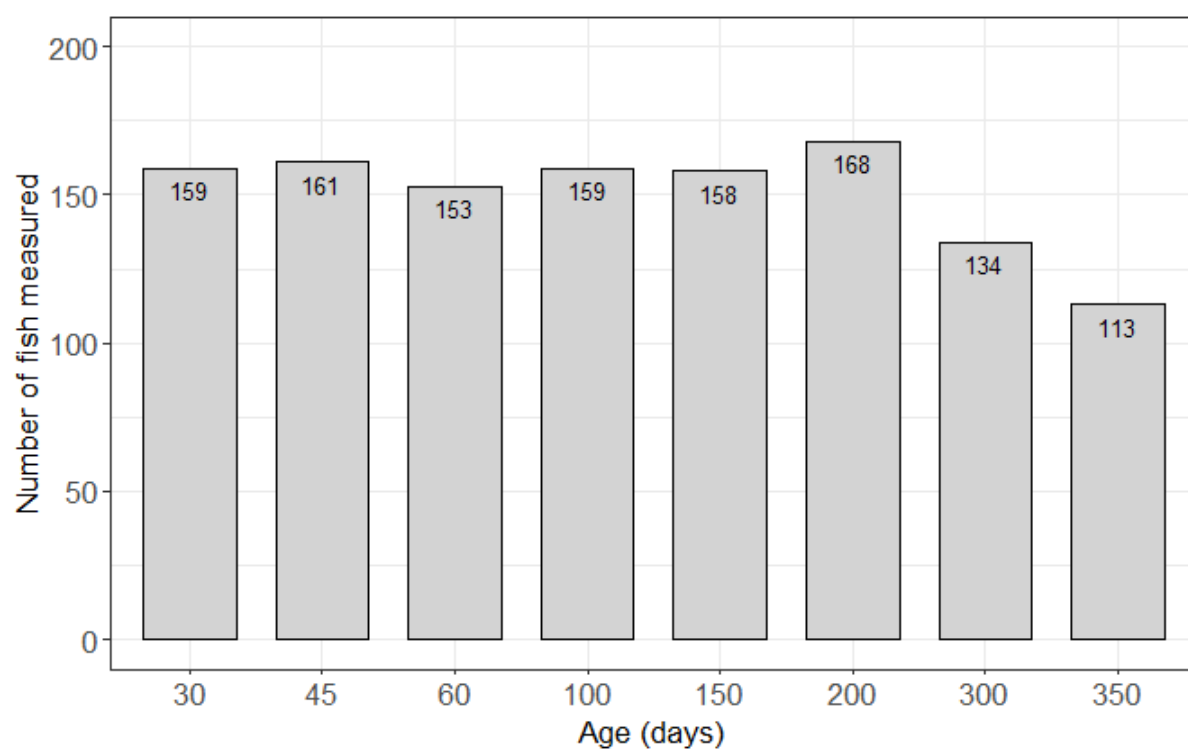
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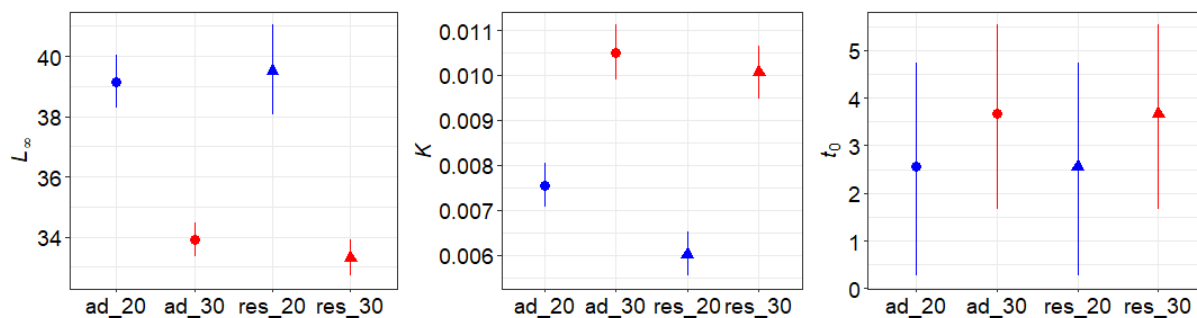
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## Appendix



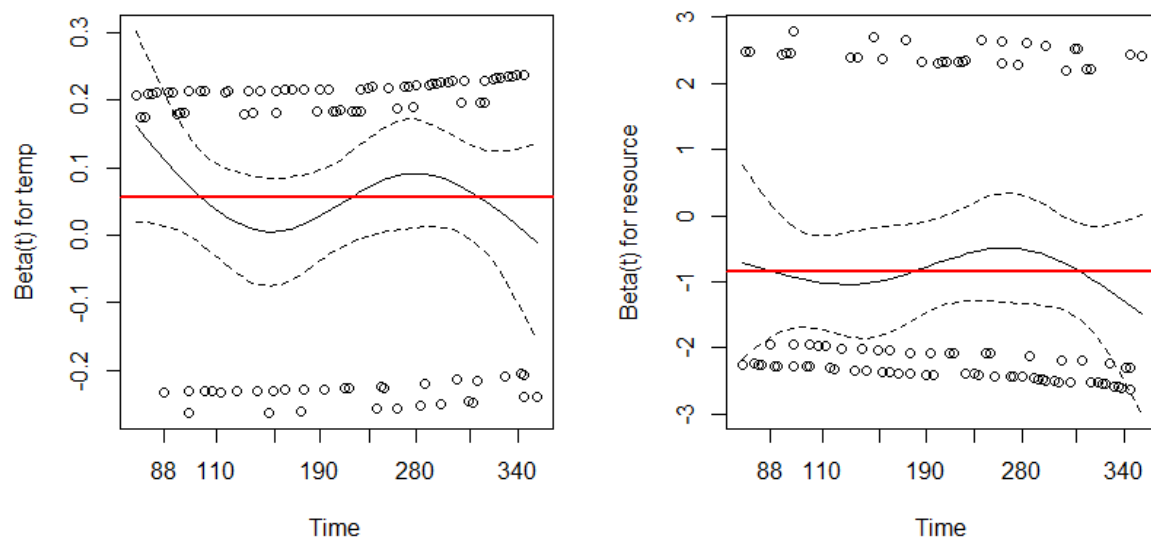
*Fig. S 1: Number of fish measured at different ages.*



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

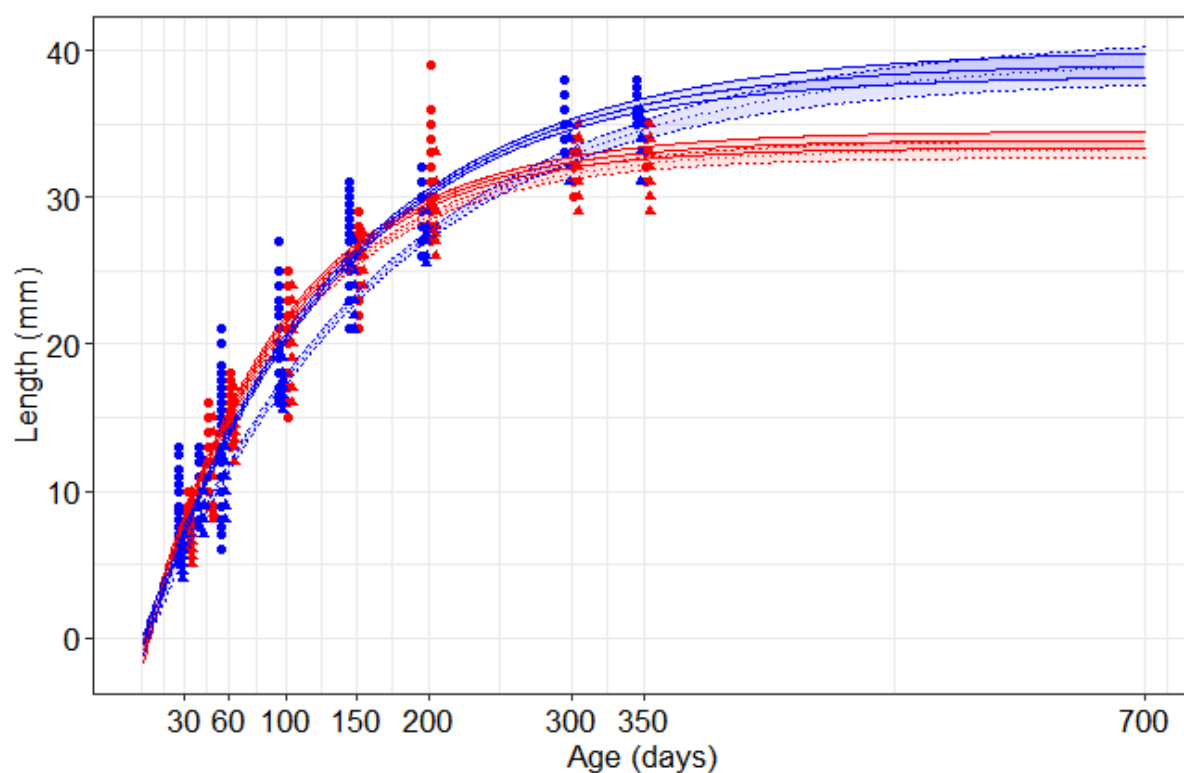
Blue and red colors correspond to the cold and warm treatments, respectively. Circles and triangles correspond to the *ad libitum* and resource restriction treatments, respectively. Bars represent 95 % credibility intervals.

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



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

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.



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