Distinct impacts of food restriction and warming on life history traits affect population fitness in vertebrate ectotherms
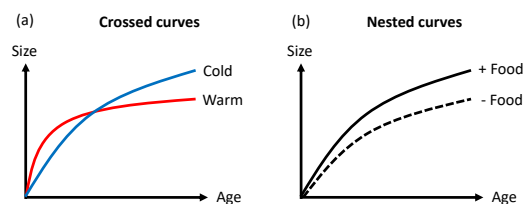
Simon Bazin[1], Claire Hemmer-Brepson[1], Maxime Logez[1], Arnaud Sentis[1], and Martin Daufresne[1]
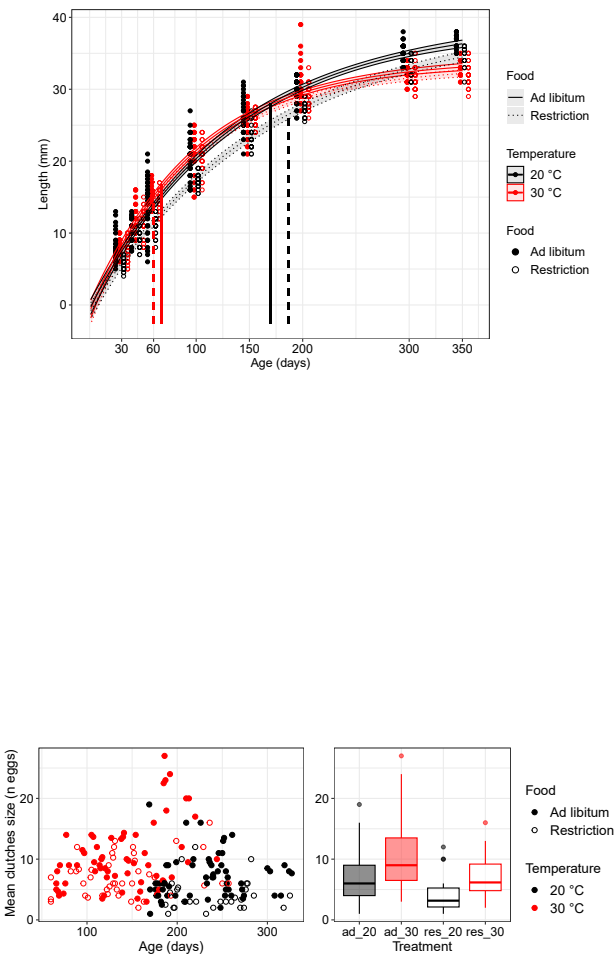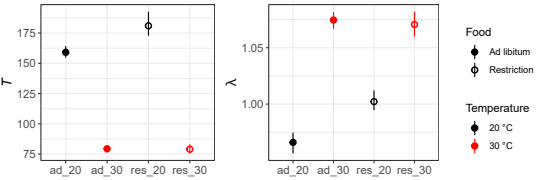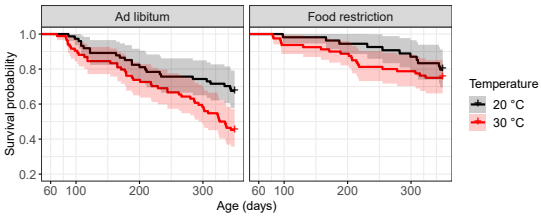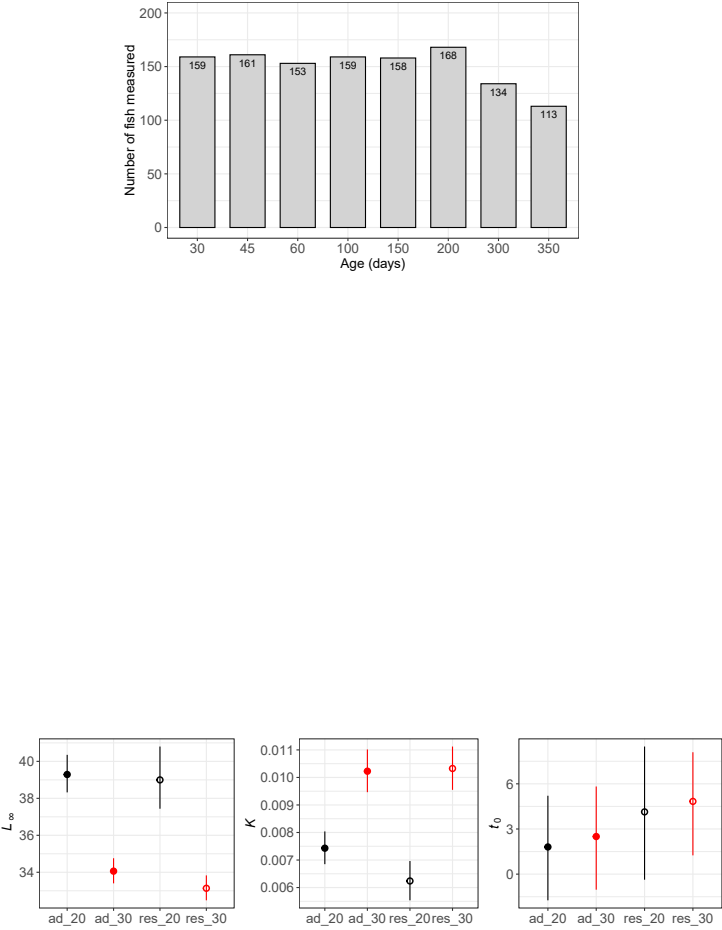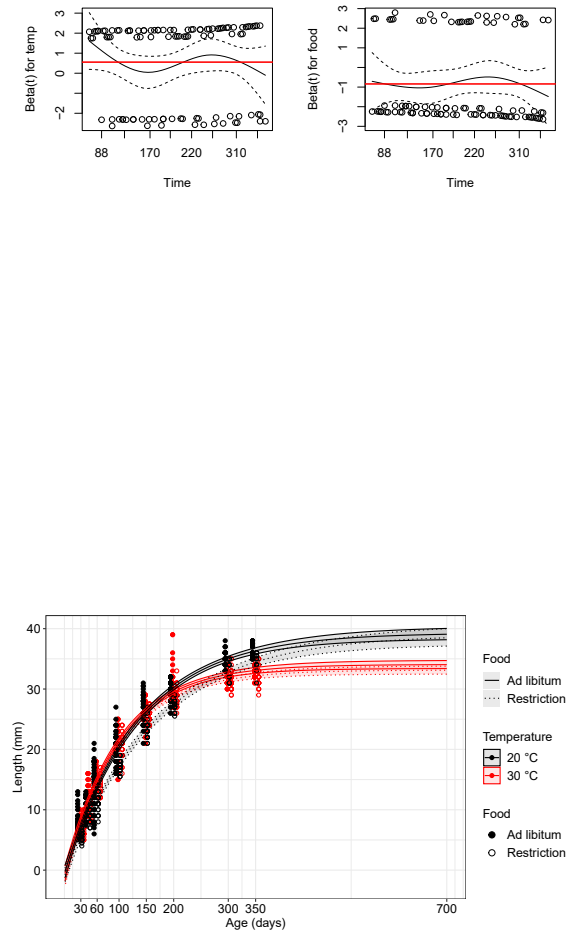
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June 7, 2023

Abstract

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 size when food availability does not limit growth. However, climate warming can decrease food availability and we have limited information on how temperature and food jointly influence life history traits and population fitness. We investigated under laboratory conditions the independent and interactive effects of temperature (20 °C and 30 °C) and food availability (restricted or ad libitum) on the growth, fecundity and survival of the medaka fish Oryzias latipes. We next used our empirical estimates of vital rates as input parameters of an Integral Projection model (IPM) to predict how modifications in vital rates translate into population demographic parameters. Warming leads to a higher initial growth rate and lower 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. 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. Food restriction increased survival probabilities under both temperature conditions. According to the IPM, warming reduces generation time and increases mean fitness in comparison to the cold treatments. Food restriction increased generation time and fitness in the cold treatment but had no effect in the warm treatment. Our results show that temperature and food interact on vital rates and population demographics. This is important in the context of global warming, as resources are expected to change with increasing temperatures.

4

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2 # population fitness in vertebrate ectotherms

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Introduction

24

25   Body size reduction has been proposed as a third universal species response to global warming

26   (Daufresne *et al.* 2009, Gardner *et al.* 2011, Sheridan and Bickford 2011), in addition to changes in

27   phenology (Visser and Both 2005) and geographic distribution (Parmesan and Yohe 2003). While the

28   first two responses have been studied extensively (Meyer *et al.* 1999), the third one has received less

29   attention despite its high prevalence and magnitude. For instance, body size can reduce up to -4 %

30   per °C in terrestrial species and up to -8 % per °C in aquatic ectotherms (Forster *et al.* 2012). Previous

31   studies focused on proximal mechanisms, (i.e. how environmental factors influence life history traits

32   by impacting physiological and developmental processes (Thierry 2005)) and ultimate mechanisms

33   related to the evolution and adaptive value of body size changes (Atkinson and Sibly 1997, Frazier *et*

34   *al.* 2001, Hoefnagel and Verberk 2015, Verberk *et al.* 2021, Walczyńska *et al.* 2015, Zuo *et al.* 2012)

35   and their variability among species and habitats (Atkinson 1994, Forster *et al.* 2012, Horne *et al.* 2015).

36   In aquatic systems, warming decreases oxygen concentration and hypoxia tends to amplify TS

37   responses, which has been interpreted as a response to limited oxygen resource (Frazier *et al.* 2001,

38   Hoefnagel and Verberk 2015, Verberk *et al.* 2021). In contrast, in terrestrial system, oxygen is less

39   limiting and other factors may be more important than oxygen concentration. For instance, the risks

40   of not completing juvenile development in time before the onset of winter strongly determine growth

41   pattern in terrestrial organisms whereas it has less influence in the growth of aquatic organisms

42   (Verberk *et al.* 2021). These differences may explain why TS responses are weaker in terrestrial than

43   in aquatic ecosystems (Forster *et al.* 2012). At the individual level, body size shift can be explained by

44   the "Temperature Size Rule" (TSR, Angilletta *et al.* 2004, Arendt 2007, Arendt 2011, Atkinson 1994,

45   Atkinson and Sibly 1997, Berrigan and Charnov 1994, Perrin 1995), which states that ectotherms grow

46   faster but reach a smaller size at a given stage of development (e.g. size at maturity or adult size) under

47   warm environment compared to colder ones, resulting in "crossed" growth curves (Figure 1). This

48   pattern of TSR remains an evolutionary puzzle (Atkinson and Sibly 1997) and body size shifts could be

49   the result of different developmental strategies. For example, a recent study showed that warming

50   accelerates growth and reproduction leading to a rapid life cycle but also a decrease in adult survival

51   in a temperate lizard species (Bestion *et al.* 2015). This study and others (Clissold and Simpson 2015,

52   Corrêa *et al.* 2021, Courtney Jones *et al.* 2015, Kingsolver *et al.* 2006, Marn *et al.* 2017, Rohner *et al.*

53   2017) suggest that it is important to investigate the links between growth trajectories and fitness

54   related traits (survival and fecundity) to better understand the underlying trade-offs and how the

55   combination of these traits may influence individual fitness and population demographic parameters.

56   However, most studies on TSR did not investigate these links (but see Corrêa *et al.* 2021, Kingsolver *et*

57   *al.* 2006, Marn *et al.* 2017) which limits our ability to detect situations in which TSR might be adaptive

58   (i.e. increase fitness) or maladaptive.

59   Besides temperature, another major factor underlying growth, reproduction and survival is

60   food availability (Boggs and Ross 1993, Giberson and Rosenberg 1992, Boersma and Vijverberg 1996,

61   Corrêa *et al.* 2021). Individuals need enough resources, as energy and material inputs, to sustain their

62   metabolic demand and optimize the allocation of energy to growth, reproduction and maintenance

63   (Lemoine and Burkepile 2012, Brown *et al.* 2004, Cross *et al.* 2015). There is a long history of researches

64   on the influence of food availability on the growth rate and fecundity of ectothermic species

65   (Rasmussen and Ostenfeld 2000, Johnston *et al.* 2002, Giberson and Rosenberg 1992, Boersma and

66   Vijverberg 1996, Corrêa *et al.* 2021). In most cases, individuals with a higher food availability have a

67   higher fecundity and have both a higher initial growth rate and a larger size at age compared to

68   individuals under food restriction. In contrast to the pattern of crossed curves driven by temperature,

69   different resource levels lead to a pattern of nested curves where the growth curve under limiting

70   resources is nested below the growth curve under unlimited resources (Figure 1). Interestingly, food

71   restriction may also be beneficial to the lifespan of organisms as this restriction reduces the production

72   of senescence-accelerating oxidizing agents during metabolism (Sohal and Weindruch 1996, Gredilla

73   *et al.* 2001, Speakman 2005), resulting in a "eat little die old" strategy. The effects of food restriction

74   on fecundity (which decreases) and survival (which increases) are thus opposite and can be explained

75   by a resources distribution to nutrient-limited processes (Corrêa *et al.* 2021). This indicates that we

should consider the effects of food restriction on multiple life history traits to better identify underlying trade-offs, fitness consequences and thus evolutionary strategies.

The interactive effects of temperature and food availability on life history traits have been studied in invertebrates such as daphnia (Betini *et al.* 2020, Giebelhausen and Lampert 2001, Wojewodzic *et al.* 2011, Persson *et al.* 2011), rotifers (Kielbasa *et al.* 2014), diatoms (Walczyńska and Sobczyk 2017), aquatic insect larvae (Giberson and Rosenberg 1992), terrestrial insects (Clissold and Simpson 2015, Corrêa *et al.* 2021, Kingsolver *et al.* 2006, Rohner *et al.* 2017, Lee and Roh 2010), fish (McLeod *et al.* 2013) and turtles (Marn *et al.* 2017). In these studies, warming generally resulted in a rapid life cycle by increasing growth rates and decreasing age and size at maturity as well as survival probabilities. However, these thermal effects were often modulated by food availability. In particular, temperature and food availability can covary and impact ectotherm life history traits. Koussoroplis and Wacker (2016) showed that the effect of food restriction on life history traits is more severe when temperature moves away from the optimal temperature. Nevertheless, these previous studies did not fully investigated how the effects of temperature and food restriction on multiple life history traits combine to influence fitness and population demographic parameters (e.g. generation time and population growth rate). This is an important limitation as we need to determine how the combination of effects on multiple traits influence fitness to understand the adaptive value of plastic and evolutionary responses to environmental factors; the latter being the focus of several studies and intense debates in the literature on TSR (see Kingsolver and Huey 2008, Fryxell *et al.* 2020, Walters and Hassall 2006, Zamudio *et al.* 1995). In addition, almost all the studies mentioned above were conducted on small invertebrate species (but see McLeod *et al.* 2013 and Marn *et al.* 2017). As a result, we have very limited information on how temperature and food availability jointly influence life history traits of vertebrate predators. This is of importance as body size changes in predatory species can alter population structure and influence trophic interaction strength and food webs stability (Emmerson and Raffaelli 2004, Sentis *et al.* 2017, Osmond *et al.* 2017, Uzsko *et al.* 2022).

101   In this study, we address this gap by experimentally investigating growth, reproduction and

102   survival probability of a vertebrate predatory species, the medaka fish (*Oryzias latipes*, Temminck &

103   schlegel), raised at two temperatures (20 and 30 °C) with and without food restriction. Our objectives

104   were to investigate whether (1) TSR is maintained under food-restricted conditions, (2) food restriction

105   modulates the effects of temperature on the growth, fecundity and survival of a vertebrate predatory

106   species and (3) the effects of temperature and food on individual traits affect fitness and demographic

107   parameters. To this end, we implemented our empirical measurements of life history traits into

108   Integral Projection Models (IPMs) to understand and predict how their combined effects determine

109   mean fitness and generation time across our different treatments of temperature and food restriction.

110   We hypothesized that warming would increase growth and fecundity but lower survival, leading to

111   rapid life cycle (short generation time). Moreover, we hypothesized that these thermal effect would

112   be modulated by food restriction, the latter would increase survival and selects for late maturation at

113   larger body size. We therefore expected that food restriction would increase the population

114   generation time. Overall, our aim was to better understand to which extent investigating growth,

115   reproduction and survival patterns could help disentangling the relative impacts of temperature and

116   resource availability on body size shifts under global warming as well as understanding the adaptive

117   values of these phenotypic responses.

118 # Material and methods

119 ## Biological system and rearing conditions

120   The medaka is a small iteroparous freshwater fish native to East Asia (Hirshfield 1980). The life

121   span of a medaka is about 2 years and its adult size varies between 30 and 50 mm (Ding *et al.* 2010,

122   Egami and Etoh, 1969). This is an eurythermal species (5 °C - 35 °C) with an optimum temperature of

123   25 °C (Dhillon and Fox 2004). At this temperature, the medaka requires only 10 to 12 weeks to reach

124   sexual maturity. Fish were maintained in the laboratory using an open water system with water supply

125   controlled by drip emitters (1 L.h^{-1}). Input water quality was maintained with mechanical, biological

126 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

127 to prevent high nitrite concentrations and maintain oxygen at saturation.

128   The parental F_0 generation consisted in a total of 76 fish (approximately 120 days old) of the

129 CAB strain provided by Carolina Biological Supply Company (Burlington, NC, USA ; from AMAGEN, Gif-

130 sur-Yvette, France) and WatchFrog (Evry, France). At reception, fish were kept for 5 days at 25 °C. Then,

131 half of the fish were placed into five 20 L tanks for the "cold" thermal regime and the other half were

132 placed into five 20 L tanks for the "warm" thermal regime. The female to male sex ratio per tank ranged

133 from 1.33 to 1.66. The tank temperatures were increased or decreased by 0.5 °C every days until they

134 reached 30 °C or 20 °C. During this acclimation period, the photoperiod was 12h: 12h (day: night) and,

135 after acclimation, it was then adjusted to 16h: 8h (day: night) which is optimal for medaka reproduction

136 (Hirshfield 1980).

137   From this F_0 generation, about 300 eggs were collected in each tank. Eggs were placed in small

138 nurseries (2.5 L) made of fine mesh and each nursery was placed in the tank where the eggs were

139 collected from (see Hemmer-Brepson *et al.* 2014, Loisel *et al.* 2019 for more details). After 30 days of

140 growth, the parents were removed and the F_1 fish larvae were reared under four different treatment:

141 ad_20 (*ad libitum* and 20 °C), res_20 (restriction and 20 °C), ad_30 (*ad libitum* and 30 °C) and res_30

142 (restriction and 30 °C). For each treatment, the growth of approximately 80 fish was monitored, except

143 for res_20 where only 54 fish could be maintained. Fish were maintained in 20 L aquaria with 20 - 30

144 fish of a single treatment. This density (less than 2 - 3 fish per liter) does not cause any stress or

145 agonistic behaviour in this species (Denny *et al.* 1991). The fish were fed with TetraMin[©] (composition:

146 47 % protein, 10 % fat content, 3 % cellulose and 6 % water) every morning (for the *ad libitum*

147 condition) or every two mornings (for the restriction condition). On each feeding days, TetraMin[©] was

148 provided to each tank until the fish no longer went up to the surface to get food. Excess food was

149 systematically removed after feeding to prevent feeding between two meals. Apart from temperature

150 and food, all the experimental parameters were similar in the four treatments.

151   The species-specific optimal thermal range for TSR is the range between the temperature at

152   which the population growth rate becomes positive, and the temperature at which population growth

153   rate is maximal (Walczyńska *et al.* 2016). Outside of this thermal range, the TSR pattern may not be

154   observed, although the TSR can be maintained for temperatures slightly above the optimal

155   temperature (Walczyńska *et al.* 2016). Yamamoto (1975) and Hirshfield (1980) reported that the

156   optimal temperature for medaka reproduction is 27 °C, suggesting that the population growth rate is

157   maximal at this temperature. Furthermore, Dhillon and Fox (2007) showed that individual growth rate

158   did not differ for medakas reared at 27 °C or 30 °C, suggesting that our experimental temperatures are

159   within the "optimal thermal range" for TSR and that our results are not the product of a response to a

160   thermal stress.

Growth, fecundity and survival

162   The total length (from the head to the tip of the caudal fin, TL) of each fish was measured with

163   a precision of 0.5 mm at 30, 45, 60, 100, 150, 200, 300 and 350 days. Fish were measured after placing

164   them on a 5 cm diameter Petri dish layered with a millimeter graph paper and filled with water. They

165   were then immediately released into their respective tank. An average of 150.6 ± 18.1 fish were

166   measured per age (see Fig. S 1 for more details). As fish were not identified individually, the growth

167   curves applies to the experimental population (i.e. one curve per treatment) and not to individuals.

168   The investment in reproduction was quantified from sexual maturity by counting the number of eggs

169   laid per female per day in each tank. The survival probability from 60 days (age of first sexually mature

170   fish), referred to as survival in this study, was monitored daily until the end of the experiment.

Statistical analysis

172   TL measurements and ages were used to fit von Bertalanffy growth curve model (Von Berta-

173   lanffy 1938):

174     $$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) (\text{eq. 1})$$

175   Where L_t is the estimated total length at time t, $L\infty$ the maximum asymptotic size (i.e. the total length

176   for fish with an ∞ age), K the initial growth rate, and t_0 the theoretical age at which body size is null.

177   Von Bertallanfy growth curves parameters ($L\infty$, K, t_0) were estimated by Bayesian inference using the

178   Bayesian software JAGS and the "R2jags" package (Su and Yajima, 2015) in R software (version 4.0.2;

179   R development Core Team). We assumed that the asymptotic size $L\infty$, the initial growth rate K, and the

180   theoretical age at null size t_0 could vary between temperature (T) and resource (C) condition.

181   Consequently, four values of $L\infty$, K and t_0 (one for each combination (CT) of temperature and resource

182   condition) were fitted. For each parameter, we used a normal uninformative prior with a mean of 0

183   and a precision parameter (inverse of the variance) of 0.001:

184    $$L_{\infty CT} \sim N(0,0.001) \quad K_{CT} \sim N(0,0001) \quad t_{0CT} \sim N(0,0.001) \quad \text{(eq. 2)}$$

185   To account for tanks (t) variability, we estimated random effects ε for each parameter using a

186   multivariate normal distribution, $\varepsilon \sim$ N(0, Σ). The covariance matrix $\Sigma_{(3,3)}$ was defined as:

187
$$\begin{vmatrix} \sigma_{L_\infty}^2 & r_1 \cdot \sigma_{L_\infty} \cdot \sigma_K & r_2 \cdot \sigma_{L_\infty} \cdot \sigma_{t_0} \\ r_1 \cdot \sigma_{L_\infty} \cdot \sigma_K & \sigma_K^2 & r_3 \cdot \sigma_K \cdot \sigma_{t_0} \\ r_2 \cdot \sigma_{L_\infty} \cdot \sigma_{t_0} & r_3 \cdot \sigma_K \cdot \sigma_{t_0} & \sigma_{t_0}^2 \end{vmatrix} \text{(eq. 3)}$$

188   With σ_{L_∞}, σ_K, σ_{t_0} the standard deviations of each random vector, one per parameter, and r_1, r_2, r_3 the

189   correlations between these vectors. We used uninformative priors with a uniform distribution for each

190   parameter of Σ, adapting the limits to the parameters (e.g between -1 and 1 for a correlation).

191    $L_{\infty CT}$, K_{CT} and t_{0CT} are thus hyperpriors (population parameters) that serve to assess parameters for

192   each tank (t) when associated with the random effects. For instance for the L_∞ parameter:

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

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

195   (j):

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

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

198
$$L_{ftj} \sim N(L_{tj}, \sigma) \atop \sigma \sim U(0,10)}\text{(eq. 6)}$$

199   To compare the growth patterns among temperature and resource conditions, we plotted the average

200   growth curves for each treatment (combination of food condition and temperature), and their

201   credibility interval (CI) using the posterior distributions of the parameters ($L_{\infty CT}$, K_{CT}, t_{0CT}) that were

202   obtained from five independent Monte-Carlo Markov Chains (see Fig. S 2 for more details on the

203   estimated parameter values). For each chain, after an initial burning of 50 000 values, 400 000

204   iterations were computed and we conserved one value every 200 iterations to limit autocorrelation

205   between estimations. The posterior distributions for each average total length at age (*L*) were thus

206   constituted of 10,000 values. The quantiles 2.5 % and 97.5 % were used to estimate credibility intervals

207   CIs. We compared the growth curves among our four experimental treatments by investigating the

208   overlap among their CIs. Curves were considered as significantly different when their CIs do not overlap

209   (Pritchard *et al.* 2017).

210   We investigated the effects of temperature, food restriction and their interaction (fixed

211   effects) on mean daily clutch size per female (log transformed) and survival probabilities using a linear

212   mixed effects model (*lmer* function in the "lme4" package (Bates *et al.* 2015)) and a mixed effects Cox

213   proportional hazards model (*coxme* function in the "coxme" package (Therneau *et al.* 2022)), respec-

214   tively, with tank as random factor. For both models, analyses of deviance using Wald tests were pro-

215   vided to test the significance of fixed parameters. We tested the assumptions of the mixed effects Cox

216   proportional hazards model using the *cox.zph* function ("survival" package (Therneau *et al.* 2022))

217   which correlates the corresponding set of scaled Schoenfeld residuals with time to test for

218   independence between residuals and time (see Fig. S 3 for more details).

Integral Projection Modelling

219

220 Integral Projection Models are discrete-time, structured population models that estimate the

221 asymptotic behaviour of populations by combining life history traits that can be discrete or continuous

222 (Levin *et al.* 2021). We used our empirical measurement of life history traits to quantify the fitness of

223 populations simulated by IPMs for our four experimental treatments of temperature and food

224 restriction. To build an IPM, the first step is to represent the life cycle of the focal species. At each time

225 step, an individual medaka has a probability *s* to survive. If it survives, it grows according to a growth

226 function *g*. This individual has a chance to reproduce according to the function *f_p*, and if it reproduces,

227 it produces a number of eggs according to the fecundity function *f_n*. In the model, the vital rates (*s*,

228 *g*, *f_p*, *f_n*) are functions of the fish body size at time *t*. The eggs have hatching and survival

229 probabilities according to the function *f_g*, and the resulting juvenile fish have a size distribution *f_d*.

230 Egg hatching rate, survival of juvenile and their size distribution are independent from the size of their

231 parents.

232 We used a similar IPM structure as in Bogdan *et al.* (2021):

233
$$n(z', t + 1) = \int_{L}^{U} K(z',z)n(z,t)dz \ (eq. 7)$$

234 Where *n(z', t+1)* is the size of the population at time *t+1*, *z'* is the state variable describing the

235 population (i.e. body size in our model). *n(z', t+1)* is obtained by integrating the product of *K(z',z)* and

236 *n(z,t)* over the domain [*L*, *U*]. In our model, the lower bound *L* is the minimum fish size and the upper

237 bound *U* is the maximum size. *K(z',z)* is a bivariate kernel function that describes the transitions to state

238 *z'* given the initial state of an individual *z* at time *t*. *K(z',z)* consists of two sub-kernels *P* and *F*. *P*

239 describes the survival and growth of fish at time *t* (*P = s · g*) and *F* describes the number and body size

240 of juveniles at time *t+1* according to reproduction probability, hatching rate, juvenile survival and body

241 size distribution (*F = f_p · f_n · f_g · f_d*).

242 This yields to:

243
$$n(z', t+1) = \int_L^U [P(z',z) + F(z',z)]n(z,t)dz \ (eq.\,8)$$

244 The analytical solutions of IPMs are very resource expensive. An alternative method to solve eq. 8 is

245 to use the integration rule of the midpoint of the meshes along the domain [*L,U*] (Ellner *et al.* 2016).

246 In our model, the domain extends from the predicted size in log of a fish after 30 days (*L*) to the

247 maximum observed size in log (*U*). The number of meshes along this domain was set to 400.

248 To obtain the survival function *s*, we used Kaplan-Meier estimate to compute the survival

249 probability for each sampled age. We then associated survival probabilities to fish body size using the

250 estimated age-size relationship from the fitted Von Bertalanffy model. Survival probability (*s*) in

251 function of body size was estimated using a logistic equation for each experimental treatment of

252 temperature and food restriction.

253 To obtain the growth function *g*, we predicted the size at t (L_t) (from 0 to 350 days) of 10,000

254 fish from the 10,000 combinations of Von Bertallanfy parameters from the Bayesian model posterior

255 distributions. We then calculated the size at *t+1* (L_{t+1}) from L_t following the formula:

256
$$L_{t+1} = L_t \cdot e^{-K} + L_\infty \cdot \left(1 - e^{-K}\right) (eq.\,9)$$

257 For each age, we computed the standard deviation of the sizes at *t+1* (10,000 values), and then

258 considered the average value of the standard deviations to implement residual variation around

259 growth (*g*).

260 For the reproduction probability (*f_p*), we used a logistic equation considering that all fish reproduce

261 once they reach their treatment-dependent age at maturity. For the fecundity function (*f_n*), we used

262 a Poisson regression model to describe the link between fish size and egg number. Egg hatching rate

263 and survival probability (*f_g*) and the body size distribution of juveniles (*f_d*) were estimated from

264 unpublished data from the same experimental populations.

265   We used the "ipmr" R package functions to define the kernels (*define_kernel*), the domain

266   (*define_domains*), and the initial state of the population (*define_pop_state*), and to compute the IPMs

267   (*make_ipm*). The number of iterations of the IPMs was fixed per treatment to achieve asymptotic

268   dynamics according to the *is_conv_to_asymptotic* function. We used the *gen_time* and *lambda*

269   functions from the "Rage" and "ipmr" R packages to quantify the generation time *T* and the asymptotic

270   *per capita* population growth rate λ. We quantified the uncertainty of *T* and λ by bootstrapping 1000

271   combinations of L_∞, *K* and t_0 from the Bayesian model posterior distributions (with replacement) and

272   by using 1000 random sample of each vital rate data set (survival, reproduction and fecundity) and

273   refitting all demographic functions *s*, *g*, *f_p*, *f_n* . For each new iteration, we ran an IPM and estimated

274   *T* and λ. This yielded 1000 estimates of *T* and λ for each experimental treatments. We next calculated

275   the 95 % confidence intervals of *T* and λ and compared their mean values across experimental

276   treatments based on the overlap of their 95 % confidence intervals. We also performed a sensitivity

277   analysis to investigate the sensitivity of *T* and λ to small changes in the vital rate estimates (see Fig. S

278   5). Data and scripts used to build the IPMs and perform the sensitivity analysis are available online.

279   Results

280   We found that, under *ad libitum* conditions, warming leads to crossed growth curves by

281   increasing initial growth rate and decreasing adult size (Figure 2). The same pattern was observed

282   under food restriction, although the curves crossed later for the food-restricted fish compared to *ad*

283   *libitum* fish. Food restriction in the cold treatment leads to nested growth curves throughout the

284   experiment by decreasing the initial growth rate and adult size. Growth curves also tended to be

285   nested in the warm treatment although the credibility intervals overlapped until day 149 and the

286   curves were only significantly different toward the end of the experiment (from day 149 to day 316,

287   Figure 2).

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

289   0.1 mm) under *ad libitum* condition and at 60 days for all replicates (body length: 17.2 ± 0.7 mm) under

290   food restriction. In the cold treatment, they were sexually mature at 169.7 ± 0.6 days (body length:

291   26.3 ± 0.6 mm) and 186.5 ± 0.7 days (body length: 25.7 ± 0.4 mm) under *ad libitum* and food restriction

292   conditions, respectively (Figure 3). We found that warming increased mean daily clutch size per female

293   (*df = 1, Chi² = 13.26, p < 0.001*) and food restriction decreased it (*df = 1, Chi² = 10.58,*

294   *p = 0.001*). Mean daily clutch size per female was not dependent on the interaction between

295   temperature and food conditions (*df = 1, chi² = 0.79, p = 0.37*).

296   The fish survival was not significantly affected by the interaction between warming and food

297   restriction (*Chi² = 0.70, df = 1, p = 0.40, n = 292*). In contrast, warming significantly reduced the fish

298   survival (*Chi² = 6.96, df = 1, p = 0.01, n = 292*). Moreover, food restriction significantly increased survival

299   (*Chi² = 15.04, df = 1, p < 0.001, n = 292*) (Figure 4).

300   We found that warming decreased generation time *T* and increased the asymptotic *per capita*

301   population growth rate *λ* (Figure 5). In the cold treatment, food restriction significantly increased *T* and

302   *λ*. Food restriction had no significant effect on *T* and *λ* in the warm treatment as their 95 % confidence

303   intervals overlapped.

304   Discussion

305   Shrinking body size with increasing temperature has been proposed as a third universal

306   response to global warming (Daufresne *et al.* 2009, Gardner *et al.* 2011). In addition, resources are

307   expected to change with global warming (De Senerpont Domis *et al.* 2014), in response to changes in

308   physicochemical, phenological (Visser and Both, 2005) and geographical parameters (Parmesan and

309   Yohe, 2003). The independent and interactive effects of temperature and food availability on life

310   history traits have been mainly studied in small aquatic (Betini *et al.* 2020, Giebelhausen and Lampert

311   2001, Wojewodzic *et al.* 2011, Persson *et al.* 2011, Giberson and Rosenberg 1992) and terrestrial

312   (Clissold and Simpson 2015, Corrêa *et al.* 2021, Rohner *et al.* 2017, Lee and Roh 2010) invertebrate

313   species. However, we have limited information on how temperature and food availability jointly

314   influence life history traits in vertebrate predators and how the integration of these traits may

315 influence population fitness. Our objective was thus to test whether food availability can modulate the

316 effects of temperature on size at age and life history traits of a vertebrate predator species, the medaka

317 fish, and to investigate how these traits can affect population demographic parameters and life history

318 strategies.

319   The results of our laboratory experiment indicate that, in agreement with the TSR rule

320 (Atkinson and Sibly 1997, Berrigan and Charnov 1994, Arendt 2011), warming leads to crossed growth

321 curves with individuals growing faster but reaching a smaller size at maturity and adult size compared

322 to the cold condition. We conducted a short synthesis of the results of previous experimental studies

323 investigating the responses in size at maturity or adult size to warming and food conditions (see Table

324 S 1). This synthesis shows the important variability in the responses of size at maturity or adult size to

325 temperature and food and the complexity of understanding the mechanisms underlying the control of

326 body size in ectotherms. In line with our results, warming generally leads to a decrease in size at

327 maturity and adult size in experimental studies (Table S 1). Nevertheless, some studies reported that

328 temperature does not affect size at maturity or adult size, or can even increase body size (Table S 1).

329 We found that food restriction does not affect size at maturity but leads to nested curves where

330 restricted fish are smaller than non-restricted fish for each given age. These results are consistent with

331 other experimental studies reporting that food restriction decreases adult size but does not affect size

332 at maturity (Table S 1). In contrast, Giebelhausen and Lampert (2001), Courtney Jones *et al.* (2015),

333 and Rohner *et al.* (2017) found a decrease in size at maturity under food restriction. Furthermore, the

334 food restriction effects appeared to be greater at 20 °C where the growth curve for the restricted fish

335 was more nested (i.e. below the curves for non-restricted fish) than at 30 °C. This is surprising because

336 we expected food restriction to have more effect in warm treatment (as reported in McLeod *et al.*

337 2013, Wojewodzic *et al.* 2011, and Persson *et al.* 2011, Giberson and Rosenberg 1992) because

338 warming increases metabolic rates which implies higher energy demand and feeding rate to sustain

339 high metabolic costs (Brown *et al.* 2004). For instance, Betini *et al.* (2020) found a TSR amplification

340 under food restriction with a body size reduction under warming five time stronger under food

341 restriction than under unlimited food conditions. Wojewodzic *et al.* (2011) and Persson *et al.* (2011)

342 also reported that warming further amplifies the decrease in somatic growth rates of Daphnia under

343 low nutritional quality (high C:P ratio) compared to Daphnia under high nutritional quality (low C:P

344 ratio). These results suggest that temperature-induced body size shifts depend on the quantity but

345 also the quality of resources with lower resource quality amplifying the detrimental effect of warming

346 as reported in a recent study (Sentis *et al.* 2022). In addition to temperature and food, oxygen also

347 appears to be a key factor controlling body size. In particular, TSR tends to be amplified under oxygen

348 limitation (Frazier *et al.* 2001, Hoefnagel and Verberk 2015, Verberk *et al.* 2021). One of the most

349 important differences between oxygen and food availability is that the former generally decreases with

350 increasing temperature, while the latter may increase or decrease with warming. Walczyńska and

351 Sobczyk (2017) suggested that TSR is a plastic response to temperature-dependent oxygen availability,

352 but that food conditions should be controlled as a factor that shapes the strength of TSR.

353 For several species, warming leads to early maturation and increased fecundity (Betini *et al.*

354 2020, Marn *et al.* 2017, Giebelhausen and Lampert 2001). Our results are in line with these studies as

355 we found that fish reared at 30 °C were sexually mature at a younger age and produced a larger mean

356 daily clutch size per female. In contrast, less is known about the responses of developmental rates and

357 fecundity to covariation between temperature and food. Our results did not suggest any effect of food

358 restriction on age at maturity, in contrast to Betini *et al.* (2020) and Marn *et al.* (2017), who found that

359 increased food availability resulted in earlier maturation. However, we found that food restriction

360 decreased mean daily clutch size at both temperature conditions. Several studies have also found that

361 increased food availability increased fecundity in both aquatic (Betini *et al.* 2020, Giberson and

362 Rosenberg 1992) and terrestrial (Corrêa *et al.* 2021) organisms. This can be explained by an increase

363 in the amount of energy to be allocated to reproduction under unlimited food conditions.

364 In addition, the survival probability in our experiment was influenced by both temperature and

365 food restriction. Indeed, fish reared at 30 °C had a lower survival than fish reared at 20 °C while food

366   restriction increased the survival under both temperature conditions. This beneficial effect of food

367   restriction on survival was also observed in frog larvae (Courtney Jones *et al.* 2015) and daphnia (Betini

368   *et al.* 2020). Lower food availability implies a decrease in metabolism and thus a lower production of

369   oxidizing agents which contributes to slow down scenescence and increase survival, resulting in a "eat

370   little die old" strategy (Sohal and Weindruch, 1996, Gredilla *et al.* 2001, Speakman 2005, Pifferi *et al.*

371   2018). Our results potentially illustrates different developmental strategies. For example, at 30 °C, fish

372   may have maintained a high growth rate despite food restriction in order to maintain a rapid life cycle,

373   at the expense of lower survival. This hypothesis is supported by the fact that mortality was higher and

374   sexual maturity was reached at a younger age and smaller size at 30 °C compared to 20 °C. Ultimately,

375   measuring the fitness of the fish under the different conditions would help understanding if these

376   strategies are adaptive or results from physiological constraints than are difficulty overpassed by

377   evolutionary adaptations.

378   Although food restriction decreased the mean daily clutch size, these effects were relatively

379   weak compared to the increase in survival. This may be explained by potential acclimation of medaka

380   to rearing temperatures or by food restriction being not sever enough. Reducing feeding events by half

381   (1 out of 2 mornings) was considered restrictive although we cannot exclude compensatory

382   mechanisms were restricted fish would feed more when they have access to food. Although this

383   remains to be investigated in more details, our results highlight the importance of considering the

384   interactions between temperature, body size and food to understand how larger predatory species

385   respond to global changes in terms of developmental and life history strategies. When we integrated

386   our experimentally measured traits into integral projection models (IPM), we found a reduction in

387   generation time and an increase in the population growth rate under warming. Although survival

388   probability was lower under warming, fish reached sexual maturity much faster and had higher

389   fecundity. The earlier sexual maturity of fish enabled them to reproduce for a longer time. Therefore,

390   each female could produce a higher number of juveniles, which leads to a higher population growth

391   rate compared to cold-acclimated populations. Consistent with our experimental data, the IPMs

392 revealed that food restriction had a greater impact on the generation time and growth rate of cold-

393 acclimated populations compared to warm-acclimated populations. Specifically, food restriction

394 increased generation time and asymptotic *per capita* population growth rate at 20 °C, whereas it had

395 no significant effect on demographic parameters of the populations at 30 °C. Our experimental results

396 showed that food restriction slightly decreased fecundity but strongly increased fish survival

397 probability, resulting in longer individual lifespans and the production of more juveniles. Ultimately,

398 food restriction proved evolutionarily advantageous in the cold treatment, leading to a population

399 growth rate equals to unity ($\lambda = 1$). This indicates that the population moves from a declining dynamic

400 ($\lambda < 1$) when food is not limiting to an increasing dynamic ($\lambda > 1$) under food restriction. Our sensitivity

401 analyses revealed that the demographic parameters were mainly sensitive to the reproduction and

402 survival probabilities (see Fig. S 5). These parameters determine the lifespan of the fish and the

403 duration of their reproduction. The high sensitivity of the model to the reproduction probability can

404 be explained by our assumption that, in the model, all females reproduce once they reach maturity

405 (because lacked information on which female reproduces when) which lead to a steep reproduction

406 function. Nevertheless, this assumption was similar for the four treatment and should not influence

407 the qualitative comparison of our four treatments. Overall, IPMs allowed for the combination of traits

408 and confirmed that population mean fitness increases with temperature, and that food restriction

409 increases mean fitness at low temperature.

410   The ecological consequences of temperature-induced changes in body size are multiple. For

411 instance, it can alter predator-prey size ratio which has important implications for the occurrence and

412 strength of predator-prey interactions and thus for community dynamics and food web structure

413 (Sentis *et al.* 2017, Yodzis and Innes 1992, Kalinkat *et al.* 2013, Vagnon *et al.* 2021, Emmerson and

414 Raffaelli 2004, Williams and Martinez 2000). Size interacts with temperature because temperature

415 alters the energetic demands of organisms. For example, higher temperatures can increase short-term

416 predator-prey interaction strength and predator energetic efficiency (Sentis *et al.* 2012). To date,

417 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, Bideault *et al.* 2019). However, our results emphasize the importance of considering ontogeny in future studies as the temperature effect on growth are dependent on life stages. In addition, we expect phenological and geographic changes to alter the quantity and quality of resources (Winder and Schindler 2004, Paerl and Huisman 2008, Paerl 2014, Ekvall *et al.* 2013, Urrutia-Cordero *et al.* 2017), for example in predator-prey relationships by inducing temporal or spatial mismatches where the predator is left with reduced food availability (Boukal *et al.* 2019, Twining *et al.* 2022). Along the same line, Visser *et al.* (2006) showed that asynchrony between caterpillar biomass and the offspring feeding requirements of an insectivorous bird affected the number and weight of fledged birds. These phenological asynchronies can alter the structure and dynamics of food webs and modify ecosystem processes (Damien and Tougeron 2019, Renner and Zohner 2018). Altogether, these studies indicate that it is important to investigate the direct effects of temperature as well as indirect effects such as altered food quality and availability to better understand the impact of climate change on growth, survival and fecundity.

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Figures legend

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

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. Vertical bars represent age at maturity. 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).

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.

Figure 4: Kaplan-Meier survival curves from 60 days 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.

Figure 5: Estimated (a) generation time T and (b) asymptotic per capita population growth rate λ for each combination of temperature and food conditions. Black and red colors correspond to the cold and warm treatments, respectively. Filled and empty circles correspond to the median of *ad libitum* and food restriction treatments, respectively. Bars represent 95 % confident intervals.

Appendix

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

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 median of *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.

Fig. S 3: Cox model assumption of proportionality for temperature and food 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 (*chi² = 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*), indicating a proportional hazards.

Fig. S 4: Extrapolation of Von Bertalanffy growth curve for each combination of temperature and food conditions. Black and red colors represent the cold and warm treatments, respectively. Solid and

767   dotted lines represent the *ad libitum* and the food restriction treatments, respectively. Areas represent

768   the 95 % credibility intervals. Points represent experimentally measured sizes at age.

769   **Table S 1:** Responses in size at maturity and adult size to warming and food increase in the

770   experimental studies. The symbols +, - and x indicate a positive, negative or no effect of the variable,

771   respectively.

772   Persson *et al.* (2011) and Wojewodzic *et al.* (2011) were not included in this table as they

773   looked at the individual somatic growth rate SGR (which differs from the size at maturity or adult size).

774   They found that SGR of daphnia increased with temperature, but that this effect depended on the C:P

775   ratio of the food. The higher the temperature, the more phosphorus limitation decreased the SGR.

776   **Fig. S 5:** Sensitivity analysis of (a) asymptotic per capita population growth rate λ *and* (b) generation

777   time *T*. Black and red colors correspond to the cold and warm treatments, respectively. Filled and

778   empty circles correspond to the median of ad libitum and food restriction treatments, respectively.

779   We performed sensitivity analyses to investigate the sensitivity of generation time *T* and the

780   asymptotic per capita population growth rate λ to small changes in the values of vital rates. To do so,

781   we added or substracted 1 % to the slope of the relationships between survival, reproductive

782   probability or fecundity and body size. For the parameters that are independent of body size, we added

783   or subtracted 1 % to the mean value. For the growth function, we also modified K and L_∞ by adding or

784   subtracting 1 % to their mean values. We then investigated the sensitivity of *T* and λ by calculating the

785   log ratio of the parameter (λ or *T*) estimated by the model with a change of 1 % in a single variable to

786   the parameter estimated by the baseline IPM model. The further the log of this ratio is away from 0,

787   the more sensitive the demographic parameter is to the vital rate.

788   Demographic parameters are most sensitive to variability in reproductive probability. Since we

789   consider all fish to reproduce with probability = 1 from sexual maturity, adding or substracting 1 % to

790   the slope of the regression is equivalent to increasing or decreasing age at sexual maturity by 13.7,

791 10.3, 2.4, and 1.8 days for conditions ad_20, res_20, ad_30, and res_30, respectively. Not surprisingly,

792 this input strongly influences the demographic parameters since in the model the length of time a fish

793 is fertile depends directly on age at maturity. Demographic parameters are also sensitive to the

794 probability of survival. As with the probability of reproduction, this survival probability also determines

795 the length of time a fish can produce eggs before it dies. Finally, the generation time is somewhat

796 sensitive to the K and L_∞ parameters of the Von Bertallanfy model. By influencing growth, these

797 parameters will determine the rate at which a fish reaches size at sexual maturity in the model, and

798 thus the rate at which a fish can reproduce, directly impacting generation time.