Journal of Thermal Biology 84 (2019) 460–468

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Variation of thermal plasticity in growth and reproduction patterns: Importance of ancestral and developmental temperatures.

Ayala Loisel[a,*], Alejandro Isla[b], Martin Daufresne[a]

[a] Irstea, Pôle d'études et recherches AFB-Irstea Ecosystèmes lacustres (ECLA), Unité de recherche RECOVER, Equipe FRESHCO, 13182 Aix-en-Provence, France
[b] Spanish Institute of Oceanography (IEO), Gijón, Spain

ARTICLE INFO

Keywords:
Fish
Growth
Life history trait
Oryzias latipes
Reproduction
Temperature-size rule

ABSTRACT

Temperature is an important ecological driver modulating life history traits of organisms, such as growth and reproduction. With the ongoing global warming, understanding the mechanisms underlying the effect of temperature on size and resource allocation trade-off is crucial. The temperature-size rule (TSR) describes plastic growth patterns in populations of ectothermic species under different thermal environments, whereby warming results in faster initial growth but lower size at maturity. However, the evolution of the TSR remains poorly understood. Here we conducted an experiment with populations of the medaka fish *Oryzias latipes* maintained at two temperatures for successive generations to investigate changes in the growth pattern of the TSR. After rearing six generations at cold (20 °C) and warm (30 °C) temperature, we conducted common garden experiments on the seventh generation where we compare growth trajectories and reproduction patterns in four different groups of fish: (i) fish reared at cold temperature over all seven generations (cold past and present), (ii) fish reared at warm temperature over six generations and at cold temperature at the seventh generation (warm past and cold present), (iii) fish reared at warm temperature over all seven generations (warm past and present) and (iv) fish reared at cold temperature over six generations and at warm temperature at the seventh generation (cold past and warm present). For each treatment, we monitored growth curves and reproduction, and investigated changes in model parameters and reproduction up to 350 days after hatching. Our study showed changes in TSR patterns according to ancestral and developmental temperatures. Developmental temperature mainly impacted age at maturity and asymptotic size, whereas size at maturity was driven more by the dissimilarity between developmental and ancestral temperatures. Our results also highlight a loss of plasticity in temperature-size and reproductive patterns for the fish that were reared under warm condition over six generations.

1. Introduction

In the global warming context, understanding the modalities and mechanisms underlying the biological and ecological impacts of changing temperature is of prime importance. Temperature is an important environmental driver that affects the life history traits and strategies of organisms at molecular, cellular, individual and populational scales (Małek et al., 2015; Parmesan, 2006; Pérez-Valencia and Moya-Raygoza, 2015; Pörtner and Farrell, 2008; Sentis et al., 2017; Walczyńska et al., 2017). Body size is strongly influenced by temperature through the relationship between metabolism (enhanced under warming), development and growth (Brown and Sibly, 2006; Hoefnagel et al., 2018; Kozłowski et al., 2004; van der Have and de Jong, 1996; von Bertalanffy, 1957). Body size is a key factor that determines life history, being linked to morphological, physiological, trophic and reproductive traits (Kozłowski et al., 2004; Ohlberger, 2013; Horne et al., 2017; Walczyńska et al., 2017).

Body size influences fecundity, and is a major determinant of fitness, especially for ectotherms (Roff, 1992; Stearns, 1992; Steigenga and Fischer, 2007; Walczyńska et al., 2015). Reduction in body size was recently recognised as the third universal ecological response to global warming, along with shifts in species geographical ranges and in species phenology (Daufresne et al., 2009; Gardner et al., 2011; Horne et al., 2017). Ectotherms, which represent 99% of living animal species (Atkinson and Sibly, 1997), are especially sensitive to global warming because of their temperature-dependent metabolism. At the phenotypic scale, warming increases growth rate, but leads to earlier maturation and smaller adult size (Atkinson, 1994). This plastic thermal response is

---

[*] Corresponding author.
E-mail addresses: ayala.loisel@irstea.fr (A. Loisel), jandro.isla@gmail.com- (A. Isla), martin.daufresne@irstea.fr (M. Daufresne).

https://doi.org/10.1016/j.jtherbio.2019.07.029
Received 4 February 2019; Received in revised form 9 July 2019; Accepted 26 July 2019

referred to as the temperature-size rule (TSR; Angilletta et al., 2004, 2003; Angilletta and Dunham, 2003; Atkinson, 1994; Berrigan and Charnov, 1994; Małek et al., 2015; Pérez-Valencia and Moya-Raygoza, 2015). The strength of the TSR depends on habitat, with aquatic species shrinking more with warming than terrestrial ones (Forster et al., 2012; Horne et al., 2015).

Body size and fecundity are often positively correlated (Honěk, 1993; Roff, 1980, 1992; Stearns, 1992). On the one hand, the TSR implies earlier maturity under warming which increases likelihood of reproducing. But on the other hand, smaller size is associated with lower fecundity, which can seem counterintuitive (Sibly and Atkinson, 1994). Within ectothermic populations, a larger body size is expected to enhance fitness, favouring larger individuals (Kingsolver and Huey, 2008). It could thus be advantageous to delay maturity if the resulting larger size increases fecundity (Atkinson and Sibly, 1997), improving the net reproductive rate (R_O) (Kingsolver and Huey, 2008). By contrast, an earlier maturity would increase the number of generations in a given time, resulting in a higher intrinsic rate of population growth (represented by the Malthusian parameter r) and thus greater fitness (also known as the "compound interest hypothesis"; Angilletta et al., 2004; Fischer and Fiedler, 2002). However, adaptive models exploring this trade-off between thermal constraint on growth and maximal size did not show that TSR patterns corresponded to a greater fitness (Atkinson and Sibly, 1997; Berrigan and Charnov, 1994). More generally, according to Angilletta et al. (2004), the compound interest hypothesis would apply to species with a constrained generation time. Otherwise, natural selection would lead to earlier maturation, and if growth is favoured by temperature, to a larger size. Yet the TSR patterns are not counter-selected. In other words, assuming the TSR evolves to maximize fitness (Czarnoleski et al., 2017; Forster et al., 2013; Forster and Hirst, 2012; Shama and Wegner, 2014), the mechanisms of this evolution and its adaptive nature remain poorly understood (Angilletta et al., 2004; Arendt, 2015, 2011; Czarnoleski et al., 2017; Kozłowski et al., 2004). Phenotypic plasticity could be *passive* (non-adaptive, due to thermal constraints, *e.g.* thermodynamic, bioenergetics) or *active* (requiring specific response of organisms, *e.g.* physiological) (Schulte et al., 2011). It has been suggested that the TSR is an adaptive phenotypically plastic response (Forster and Hirst, 2012; Ghosh et al., 2013; Partridge et al., 1994; Partridge and Coyne, 1997; Steigenga and Fischer, 2007). To test this hypothesis, recent studies suggested using common garden experiments designed to test for parental and progeny responses to crossed thermal treatments in order to examine genetic and environmental effects on different traits (Forster et al., 2013, 2012; Steigenga and Fischer, 2007).

As originally defined, the TSR describes "*the direct effects of rearing temperature on the size of ectotherms at any given stage of development*" (Atkinson, 1994). From this viewpoint, it has mainly been investigated by submitting individuals of one generation to different temperatures. However, comparisons of TSR patterns between individuals with different ancestral thermal conditions (*i.e.* over several generations) are scant (but see Blanckenhorn, 2015; Forster and Hirst, 2012; Steigenga and Fischer, 2007; Walczyńska et al., 2015). Plasticity experienced by parents may span generations and act on phenotypes of offspring through transgenerational plasticity (Schulte et al., 2011). It can be considered as evolutionarily selected or even as an "anticipatory maternal effect" to prepare and protect progeny from constraints ahead (Blanckenhorn, 2000; Shama et al., 2016; Shama and Wegner, 2014; Walczyńska et al., 2015). Steigenga and Fischer (2007) state that parental effects can be a major mediator of phenotypic plasticity and might have antagonistic effects on fitness components such as egg size and body mass. However, their work only dealt with early stages, and so could not predict the fitness of progeny. The TSR predicts faster initial growth and larger size at early stages with warming, but a shorter total period of growth, leading to a lower adult body size. Studies on adults tend to focus only on growth function, and overlook reproduction, even though these two processes are related (Arendt, 2011; Kindlmann et al., 2001).

Besides the uncertainties stated above, the adaptive nature of the TSR patterns remains underexplored in vertebrates. In this work, we investigated, for the first time to our knowledge in aquatic vertebrates, whether the plasticity of the TSR patterns (usually observed for individuals of a given generation submitted contrasting temperatures) changed after long-term exposure to different temperatures. To study the importance of ancestral (past, over-generations) *vs.* developmental (present) temperature on TSR pattern, we examined the growth and reproduction of a fish model species, the Japanese medaka (*Oryzias latipes*), after several generations reared in different thermal conditions (warm *vs.* cold). To test the plastic response to each thermal condition, we designed common garden experiments (Crozier and Hutchings, 2014). We used a full factorial design with two ancestral (past) temperatures and two developmental (present) temperatures resulting in four temperature treatments: progeny from cold parents in cold conditions (cold past – cold present), progeny from cold parents in warm conditions (cold past – warm present), progeny from warm parents in warm conditions (warm past – warm present), and progeny from warm parents in cold conditions (warm past – cold present). We recorded body size throughout development, and analysed growth curves using the von Bertalanffy model. Because adult body size differs according to stage in indeterminate growers, we compared size at maturity and asymptotic size. We also investigated individual reproduction by assessing age at maturity, phenology and fecundity.

Arendt (2011) suggested that the TSR is adaptive if the slope of the relationship between size (x-axis) and fecundity (y-axis) becomes shallower with warming, as this implies smaller gains in fecundity for larger adults in warmer water. We tested this hypothesis by comparing the size-fecundity relationship among temperature treatments.

We sought (i) to determine whether the phenotypic plasticity between different thermal treatments still appeared after several generations of progeny reared under the same conditions as their parents (comparison of warm past – warm present *vs.* cold past – cold present growth and reproduction patterns), (ii) to test whether the TSR patterns were conserved (*i.e.* similar reaction norms independent of the ancestral temperature), and conversely (iii) to test for changes in the amplitude of reaction norms depending on ancestral temperature, and finally (iv) to test whether growth and reproductive patterns followed the size-fecundity relationship hypothesised by Arendt.

2. Materials and methods

2.1. Biological model

The Japanese medaka (*Oryzias latipes*) is a eurythermal rice fish species of the Adrianichthyidae family, native to marshes, ponds and rice paddies of East Asia (Leaf et al., 2011; Takehana et al., 2004). It is often used as a biological laboratory model (Fabacher and Little, 2000; Leaf et al., 2011; Overstreet et al., 2000). Its lifespan is about one year in the wild, but it can live for up to five years in captivity (Leaf et al., 2011; Shima and Mitani, 2004). It is oviparous (Shima and Mitani, 2004), matures at about 75 days post-hatching (dph) (76 – 77 dph at 26.5 °C (± 2.2, SD) (Leaf et al., 2011); 10–12 weeks (70 – 84 dph) at 27 °C (Hirshfield, 1980)) and reaches its maximum egg production at 85–92 dph at 26.5 °C (± 2.2) (Leaf et al., 2011). Its thermal optimum is 25 °C (Kirchen and West, 1976; Leaf et al., 2011), but it can survive over a wide range of temperatures (0 – 40 °C; Leaf et al., 2011; Shima and Mitani, 2004; Yamamoto, 1975), making it an ideal model for experimental non-stressful thermal studies.

2.2. Experimental design

The experiment started with a F0 of 76 individual Japanese medakas (46 females and 30 males of CAB strain) obtained from Carolina Biological Supply Company (Burlington, NC, USA; from AMAGEN, Gif-

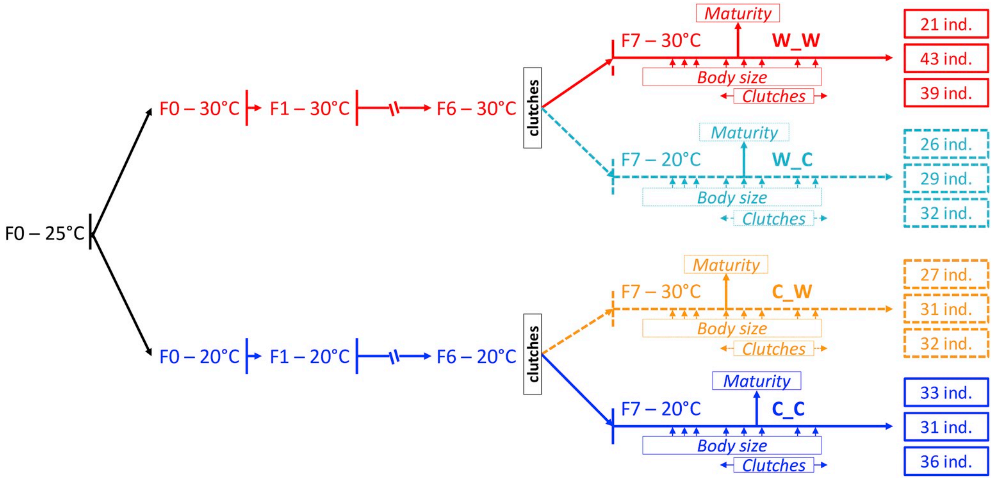

Fig. 1. Experimental design. All individuals were derived from the same parental group F0 and were reared over 6 generation at two contrasting temperatures (20 °C and 30 °C). Eggs from parents of the sixth generation were collected to carry out a common garden experiment with four treatments: warm lines (W_W; red line), cold line (C_C; blue line), cold of warm origin (W_C; dashed turquoise line) and warm of cold origin (C_W; dashed orange line). Body size at ages, maturity and egg production (clutches) were monitored for each fish tank. Monitoring periods are represented by boxes with trait name (*e.g.* body size). Arrows stand for data collected at specific age during individual life. Maturity arrows are shifted to scale with the life of individuals according to the treatment (*e.g.* C_W individuals reproduce earliest). Boxes on the right represent replicates per condition with number of individual per tank. FX = generation X. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

sur-Yvette, France) and WatchFrog (Evry, France). Fish were separated and reared at two temperatures, cold (ca. 20 °C) and warm (ca. 30 °C) (Hemmer-Brepson, 2013; Hemmer-Brepson et al., 2014) for six generations (Fig. 1). Each new generation ($n+1$) started from egg clutches laid by females from the previous generation (n), harvested around optimum fecundity (*i.e.* when the average number of eggs per female per day was at its maximum). Eggs are naturally attached to the female body. They were therefore collected directly on the female using a brush in the morning so that they could be placed in their new environment shortly after fertilization (a few hours at most). Eggs collected from females of the same condition (either cold or warm) were mixed to compose replicates of the new generation. Each generation was made up of 12 tanks (6 tanks/replicates per condition; 25 × 40 × 20 cm). Replicates (*tank*) were initially composed of hundreds of fish larvae from the same treatment randomly placed in a fish net (*nursery tank*), resulting in ca. 30 adults per tank with a 50/50 sex ratio. Density varied according to juvenile mortality, but remained low enough to minimize competition effects under unlimited food conditions (Magnuson, 1962) and to avoid agonistic behaviour (Hemmer-Brepson, 2013; Hemmer-Brepson et al., 2014).

We used a full factorial design with two ancestral (past) temperatures and two developmental (present) temperatures. We focused on the seventh generation, started from eggs laid by the females of the sixth generation during their reproduction optimum (137.51 ± 32.14 dph under the warm condition and 198.14 ± 2.80 dph under the cold condition). Collected eggs were split into nursery tanks of the two treatments, composed of a cold and a warm common garden. The cold common garden consisted of three tanks containing progeny from cold parents (cold past and cold present, C_C) and three tanks containing progeny from warm parents (warm past and cold present, W_C). Symmetrically, the warm common garden consisted of three W_W (warm past and warm present) and three C_W (cold past and warm present) tanks (Fig. 1). Growth and reproduction were monitored from 30 dph and from maturity (first egg-laying), respectively, to 350 dph (based on the average hatching time of individuals in the tank). Since temperature accelerates development, warm and cold generations were time shifted. Experiment and data sampling therefore lasted about 600 days.

Apart from temperature, all the experimental parameters were similar in the two conditions. We used an open water system, water supply being ensured by drip emitters (1 L. h^{-1}). Input water quality was maintained with mechanical, biological and UV filtration. Each tank was equipped with air powered filters to prevent any nitrite spike and maintain oxygen at 100% saturation. Fish were fed *ad libitum* with dry flake for tropical fish TetraMin© (Shima and Mitani, 2004) twice a day (9:00 h and 18:00 h). Photoperiod was set to 16 h : 8 h light : dark to maximize reproduction (Denny, 1991; Hemmer-Brepson et al., 2014; Hirshfield, 1980). Water temperature was maintained at 20 °C (± 0.63, SD) and 30 °C (± 0.52) using submersible aquarium heaters with thermostats (JUWEL©) (Fig. S1). Room temperature was adjusted to 20 °C using air conditioning. The tanks were cleaned every day to remove food leftovers and faeces.

2.3. Monitoring of life history traits

2.3.1. Growth

Size was measured at 30, 45, 60, 100, 150, 200, 300 and 350 dph. At each date, we randomly chose 15 fish from each tank and measured their total length (L_t, from head to end of caudal fin) by placing them in a Petri dish on 1 mm graph paper, with a precision of ± 0.5 mm.

Growth was modelled using the von Bertalanffy (Cailliet et al., 2006; Leaf et al., 2011; von Bertalanffy, 1960) model:

$$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right),$$

where L_∞ stands for the asymptotic size, k the growth coefficient corresponding to the initial growth rate, t time, and t_0 the theoretical initial age. Growth curves and parameters were estimated using non-linear least squares with the R package *fishmethods* (Nelson, 2017), with the same initial theoretical parameters in all cases (previous assays with theoretical parameters estimated for each tank showed no differences; Table S.2) (Quinn and Deriso, 1999). All theoretical parameters were estimated by fitting the von Bertalanffy model to all data regardless of treatment (Table S.3). Theoretical L_∞ was defined as the maximal length reached. Theoretical k was estimated by the slope of the linear regression model fitting overall body size as a function of age. Theoretically, t_0 can be before birth, *i.e.* be negative, starting when the egg is fertilized to modify the inflection point of the curve (Hoefnagel et al., 2018), but it was not possible to assess early stage data (*i.e.* larvae) in our study. Here theoretical t_0 was defined as the smallest sampled age (30 days).

2.3.2. Reproduction

Fecundity (*Fec*) was defined as the number of eggs laid per female per day in each tank. *Fec* and L_t of hatching females were monitored every morning from maturity to 350 dph in each tank. Phenology was described by the density of eggs by age specific to each treatment representing the lifetime evolution of egg laying events for each treatment.

2.4. Statistical analysis

We analysed treatment effect on growth (L_∞, k) using likelihood ratio tests (Kimura, 1980). The likelihoods of two sub-models (considering a common L_∞ value or a common k value) were compared to the likelihood of the general model (including one L_∞, one k, and one t_0 for each treatment). We computed a nonlinear mixed-effects (NLME) model taking into account all treatments following the sub-models hypothesis with tank as group effect and parameter $L_{\infty 1}+k_1+t_{01}$ as random effect (Table S.1). Differences among treatments were then tested by comparison of NLME sub-models using subsets of the data of two treatments (Table S.4).

Variability of phenology among treatments was analysed by comparing pairs of distributions with Kolmogorov-Smirnov tests.

Treatments and size effects on fecundity were analysed by a generalized linear mixed model (GLMM) with a negative binomial distribution (R package *glmmADMB;* Bolker et al., 2012; Skaug et al., 2014) according to the recommendations of Zuur et al. (2013) with *Fec* as dependent variable, *treatment,* L_t and the *treatment:*L_t interaction as fixed effects, and *tank* as random effect to control for potential within-treatment variability. *Age* was not considered because of its high correlation with L_t (Pearson correlation coefficient = 0.73, t = 90.7, $P < 2.2\text{e-}16$). Best models were selected based on their relative *AICc*.

Treatments' effects on age and size at maturity were analysed using Nested Anovas (R package *nlme;* Pinheiro et al., 2017). *Post hoc* analyses were performed to highlight differences between treatment (function *glht* of the R package *multcomp*; Bretz et al., 2016; Hothorn et al., 2008).

All statistical analyses were computed using R (R Core Team, 2017). For all tests, the significance threshold was $P = 0.05$. Normality of variables was evaluated with the Shapiro test (Royston, 1995) and visually with a quantile-quantile plot (QQplot) (Becker et al., 1988). Homoscedasticity was tested with the Bartlett test (Bartlett, 1937).

3. Results

3.1. Growth

Growth curves varied significantly among treatments of the seventh generation (Fig. 2A, Table 1). The TSR patterns were clearly visible on comparing growth curves between the two developmental thermal conditions. The complete model (H0) was selected as the best model, compared with sub-models revealing a significant effect of treatments for both k and L_∞ (Table 1). k values were significantly different among treatments (Fig. 2B left). Individuals under warm developmental conditions (W_W and C_W) had the highest k values (mean ± SD: 0.0132 ± 8e-04 and 0.0163 ± 5e-04, respectively) and the lowest L_∞ (36.36 ± 0.82 and 33.72 ± 0.4 mm) (Fig. 2B right), whereas individuals under cold developmental condition (W_C and C_C) presented the highest L_∞ (41.35 ± 1.12 and 43.82 ± 2.31 mm, respectively) and the lowest k values (0.0079 ± 3e-04 and 0.0059 ± 6e-04).

However, treatments sharing developmental temperature but with different ancestral temperatures did not display identical growth patterns, showing a significant effect of ancestral temperature (Fig. 2A and B). For both developmental temperatures, individuals with the same ancestral and developmental temperatures (W_W and C_C) exhibited significantly lower k than the crossed treatments with different ancestral temperatures *i.e.* compared to C_W and W_C respectively (Fig. 2B left). The strongest TSR pattern, characterized by the largest differences in k and L_∞ between treatments, was observed between C_W and C_C, whereas W_W and W_C showed intermediate patterns (Fig. 2A and 2B).

3.2. Reproduction

Different reproduction strategies appeared according to the ancestral and developmental temperatures (Figs. 3 and 4).

Individuals of the seventh generation under warm developmental temperature (W_W and C_W) matured earlier than those under cold (C_C and W_C) (Fig. 3A). They also displayed advances in reproductive phenology with earlier fecundity peaks and reproductive senescence than individuals experiencing cold developmental temperature (Fig. 4A).

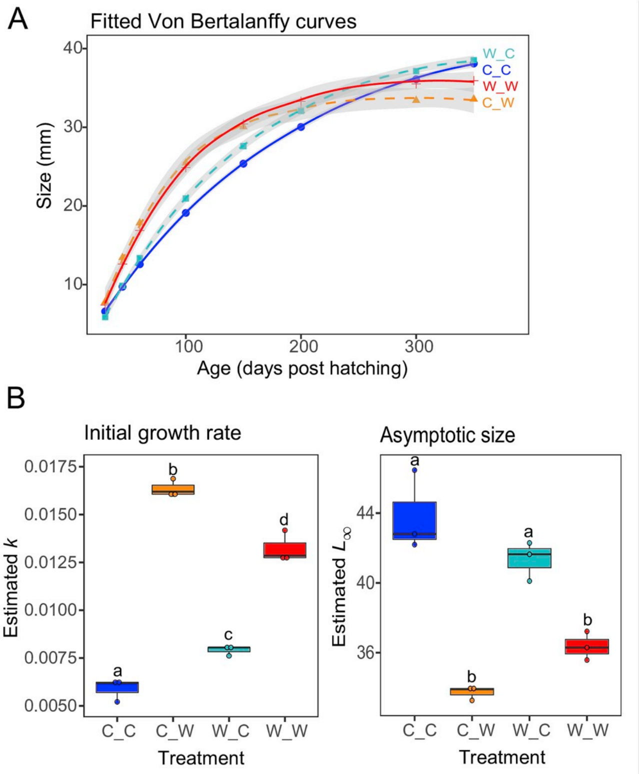

Fig. 2. Growth pattern. (**A**) Von Bertalanffy growth model curves for each treatment: warm line (W_W; continuous red line), cold line (C_C; continuous blue line), cold of warm origin (W_C; dashed turquoise line), and warm of cold origin (C_W; dashed orange line). Darkened areas around curves represent confidence interval. (**B**) Boxplots of estimated von Bertalanffy parameters. Boxplots represent the median (middle line), the first and third quantiles of the result, and points represent the measure for each replicate (tank). Boxes with different letters indicate significant differences tested by *post hoc* analyses, using NLME models and likelihood ratio tests. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Reproductive strategies of individuals sharing developmental temperature but with different ancestral temperatures (C_W, W_W and W_C, C_C) were likewise not identical, demonstrating a significant effect of the interaction with the ancestral temperature. Reproduction of C_W individuals started earliest (W_W: $D = 0.23$; W_C: $D = 0.37$; C_C: $D = 0.48$; $P < 2.2\text{e-}16$ in the other three cases) at 72 dph (df = 8, $F = 198.25$, $P < 0.0001$; Fig. 3A) with the smallest size at maturity of 22 ± 1 mm (df = 8, $F = 10.870$, $P = 0.0034$; Fig. 3B). W_W individuals started and stopped reproducing after C_W individuals, but before W_C (Kolmogorov-Smirnov test, $D = 0.31$, $P < 2.2\text{e-}16$) and C_C ($D = 0.52$, $P < 2.2\text{e-}16$) individuals (Figs. 3A and 4A). Peak of reproduction in W_C individuals occurred before that of C_C individuals, which came latest ($D = 0.38$, $P < 2.2\text{e-}16$).

Fecundity was also significantly affected by *treatment, i.e.* interaction between developmental and ancestral temperature (Table 2). We observed a rising trend in *Fec* (clutch size) with the ancestral warm condition (W_W and W_C) (Table 2; Fig. S.2C and S.3). W_W individuals had the highest mean *Fec* (11.19 ± 6.32 eggs per clutch), followed by W_C (7.72 ± 4.29 eggs per clutch, z-value = 3.65, $P = 0.0013$), C_C (6.24 ± 4.06, z-value = 5.42, $P < 1\text{e-}04$) and C_W individuals (6.18 ± 3.95 eggs per clutch, z-value = 5.59, $P < 1\text{e-}04$).

Table 1

Comparison of growth sub-models. Hypothesis H0, H1 and H2 represented sub-models following Kimura (1980) to fit length and age, with H0 as the general model (one different L_∞, k, and t_0 for each treatment), H1 as the sub-model with the same L_∞ for each treatment, and H2 as the sub-model with the same k for each treatment. The *P*-values for the effect of each model were calculated by ANOVA of the NLME. Key: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '' 1.

Property/trait	Test	Hypothesis	df	AIC	BIC	LogLik	L.Ratio	P
Growth	H0 *vs.* H1	$L_{\infty 1} = L_{\infty 2} = L_{\infty 3} = L_{\infty 4}$	19	6162.31	6262.09	−3062.16		
			13	6184.15	6252.41	−3079.07	33.84	< .0001 ***
	H0 *vs.* H2	$k_1 = k_2 = k_3 = k_4$	19	6162.31	6262.09	−3062.16		
			16	6217	6301	−3092.26	60	< .0001 ***

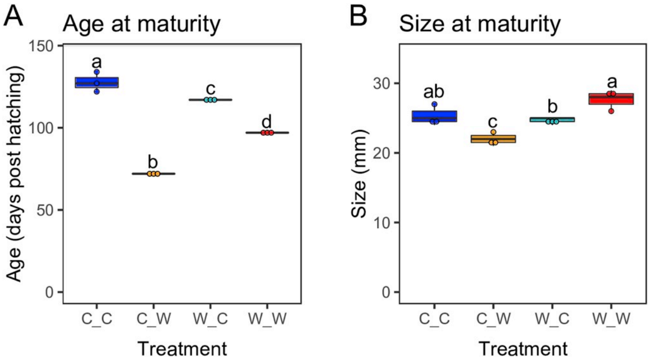

Fig. 3. Maturity features. (**A**) Age at maturity. (**B**) Size at maturity. Boxes with different letters indicate significant differences tested by *post hoc* analyses. Points represent replicate (tank) per treatment.

Fec increased with L_t for all *treatment*, but the amplitude depended on interaction between developmental and ancestral temperature (Fig. 4B, Table 2). Size-fecundity relationships were steeper for individuals with the same developmental and ancestral temperatures (W_W and C_C) than for those whose developmental temperature differed from the ancestral temperature (C_W and W_C respectively). The fecundity of W_W and C_C individuals rose with L_t (slope = 1.20 and 1.30 respectively) more than 4 times faster than for C_W individuals (slope = 0.27) and ca. 1.3 times faster than for W_C ones (slope = 0.95) (Fig. 4B).

4. Discussion

In this study, we found that the TSR patterns of faster growth, earlier maturity and smaller adult size under a warmer developmental environment persisted after six generations of exposure to different ancestral temperatures (*i.e.* comparing W_W and C_W to C_C and W_C). As reported in previous fish studies (Donelson et al., 2016; Kuparinen et al., 2011), we also found that earlier maturity under warming was associated with earlier reproduction peaks. This advance in phenology with warming is consistent with previous studies of thermal effects on fish reproduction, and may represent a rapid way to adapt to new climatic conditions (Donelson et al., 2016; Kavanagh et al., 2010; Munday et al., 2009; Salinas et al., 2013; Walczyńska et al., 2017). Other important life-history characteristics, namely size at maturity and fecundity showed no similarities between treatments sharing the same developmental temperature, but common patterns appeared between treatments sharing the same ancestral temperature (W_W, W_C and C_C, C_W). Thermal history thus offers a new perspective for understanding TSR patterns. More precisely, pairwise comparisons among the different temperature treatments revealed consistent TSR patterns between continuous treatments (C_C *vs.* W_W), crossed treatments (C_W *vs.* W_C) and treatments with the same ancestral temperature but different developmental temperatures (C_C *vs.* C_W and W_W *vs.* W_C). This conservation of the TSR patterns showed that plastic abilities persisted after long-term exposure and were regulated by developmental and ancestral temperatures for growth and reproductive traits.

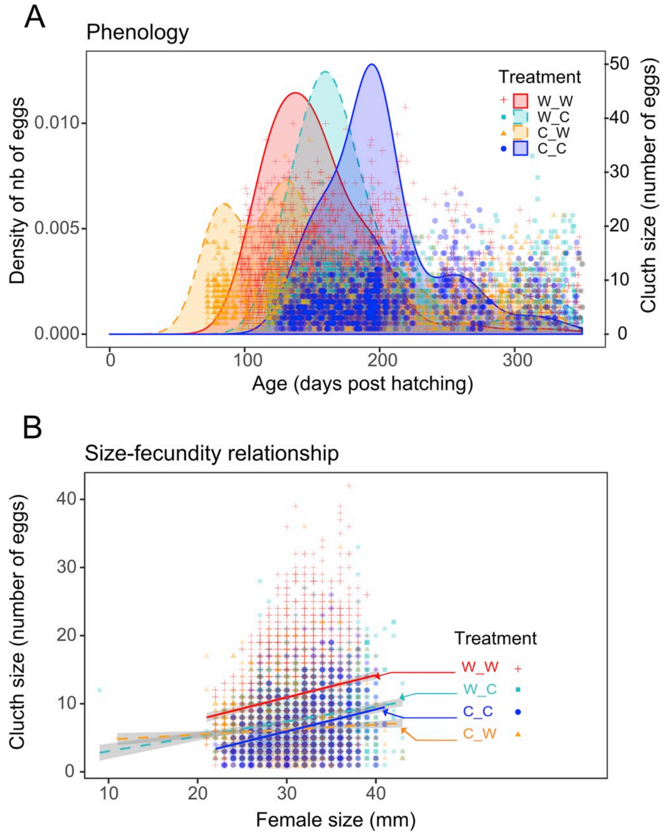

Fig. 4. Reproduction pattern. (**A**) Reproductive phenology represented by density of egg-laying events according to age for each treatment: warm lines (W_W; continuous red line and cross), cold line (C_C; continuous blue line and circle), cold of warm origin (W_C; dashed turquoise line and square) and warm of cold origin (C_W; dashed orange line and triangle). (**B**) Size-fecundity relationship for each treatment. Linear regression lines are represented with confidence intervals (grey). Points symbolize clutch size according to female size. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Another interesting finding is that the TSR pattern of smaller size under warming depended on whether we considered size at maturity or final size (*i.e.* asymptotic size). For size at maturity, the developmental temperature alone was not enough to explain individual strategies, since individuals sharing warm developmental temperature showed the greatest difference in size (*i.e.* smallest size for C_W individuals and largest for W_C). By contrast, final asymptotic sizes were smaller for fish sharing warm developmental condition (C_W and W_W) and larger for fish sharing cold developmental condition (W_C and C_C). However, considering the ancestral temperature, we found that asymptotic size in crossed treatments (C_W and W_C) tended to be smaller than in continuous treatment (C_C and W_W respectively) though not significantly so (Fig. 2B right and Fig. S.2D). Thus, size at maturity was more strongly influenced by the interaction between developmental and ancestral temperatures, *i.e.* constant thermal history *vs.* different

Table 2
Best estimation of reproduction models. The *P*-values for the effect of each model were calculated by ANOVA of the model. Key: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '' 1.

Property/trait	N	Model type	Dependent variable	Random effects		Fixed effects		
				Effect	s.d.	Effect	Chisq	*P*
Reproduction	7251	GLMM NB	*Fec*	tank	0.13	intercept	546.8	< 2.2e-16 ***
						treatment	44.2	1.373e-09 ***
						L_t	139.7	< 2.2e-16 ***
						treatment: L_t	62.6	1.607e-13 ***

developmental temperature from the ancestral one, while asymptotic size was mainly impacted by developmental temperature. Transgenerational studies on marine sticklebacks showed an increase in body size with age in a cold developmental environment, supporting our findings (Shama et al., 2014; Shama, 2015; Shama and Wegner, 2014). However, body size monitoring was stopped before maturity (*i.e.* 90 dph), limiting comparison with our work and its contribution to understanding of TSR. A study with an experimental design closer to ours on *Drosophila melanogaster* reported larger adult size for an adapted cold line (cold ancestral temperature) at cold developmental temperature (equivalent of C_C *vs.* W_C in our study), but also at warm developmental temperature (equivalent of larger adults in C_W than in W_W) unlike our results (Partridge et al., 1994). However, *Drosophila* has determinate growth (size at maturity and final size are the same) unlike medaka fish, which as indeterminate growers have to trade off the switch to reproduction (size at maturity) and somatic investment (final size) to maximize fitness. Here we focused mainly on asymptotic size, but the TSR is usually addressed through size at maturity (Brans and Meester, 2018; Breckels et al., 2013; Fischer and Fiedler, 2002; Hirst et al., 2015; Hoefnagel et al., 2018; Majdi et al., 2019; Trip et al., 2014). Maturity and stage after maturity appeared to be a key period impacted differently by temperature according to species, resulting in potentially different life trade-offs and strategies (Walczyńska et al., 2015). Our study thus highlighted the complexity of the TSR patterns and the importance of considering diverse body size metrics (*i.e.* size at maturity and asymptotic size) and thermal history (developmental and ancestral temperatures) to better understand TSR patterns in species with indeterminate growth.

We found that fish from warm ancestral and developmental temperatures (W_W) had the largest size at maturity (Figs. 3B and 2B) and the highest fecundity (Fig. S.2C and S.3), notably at an early age (Fig. 4A). According to the maximization fitness hypothesis (Kozłowski, 1999), this corresponds to the most optimal strategy (*i.e.* reproducing as much as possible at the earliest age). However, their asymptotic size was one of the smallest, bearing out that "bigger is not always better" (Fuxjäger et al., 2019; Kaplan, 1992). The fact that reproduction was higher for individuals from warm ancestral treatments is in line with previous studies on flies (Partridge et al., 1995) and coral reef fishes for relative warming (Donelson et al., 2016; Munday et al., 2017). Previous studies showed that mothers can "act" through non-genetic inheritance by investment in offspring to anticipate their future environment (transgenerational plasticity, bet-hedging, silver spoon effect) (Bonduriansky et al., 2012; Donelson et al., 2018; Engqvist and Reinhold, 2016; Fuxjäger et al., 2019; Shama, 2015, 2017).

Homogeneous lines (C_C, W_W) tended to adopt "cold strategies" if we compare with crossed treatment sharing developmental condition (W_C, C_W respectively). These "cold-slow" life-history strategies are characterized by a lower *k* and a later maturity than sharing developmental crossed treatments (C_C *vs.* W_C and W_W *vs.* C_W) and a higher L_∞ (W_W *vs.* C_W). We were unable to highlight any significant differences in L_∞ between C_C and W_C individuals. If a crossing occurred in growth trajectories, it probably did so at around 350 dph, *i.e.* at the end of our experiment (Fig. 2A). In addition, our statistical power might be too low given of the small number of individuals considered. Patterns in L_∞ were the only ones that were not consistent across the treatments and the commonly observed negative relationship between *k* and L_∞ (Atkinson and Sibly, 1997; Berrigan and Charnov, 1994) would suggest that W_C and C_C may cross. However, longer experiments involving more individuals are needed to test this hypothesis. The modification of the size-fecundity relationship (Arendt, 2011) might explain this change in growth and reproduction towards "cold" strategies. However, Arendt's assumptions have not been positively verified, since the size-fecundity slope did not drop with temperature. The slope instead dropped with a change in thermal conditions after a long-term exposure to a specific temperature (C_C *vs.* C_W; W_W *vs.* W_C), whatever the direction of the thermal change (warming or cooling). Duration of thermal exposure might thus be a major driver of the size-fecundity relationship. Parental and grandparental environment influence phenotypic plasticity of offspring fish as shown in experiments on guppies (Roy et al., 2017) and sticklebacks (Shama and Wegner, 2014). Number of generations could play a role in anticipatory strategy if transgenerational plasticity accumulates at each generation (Shama et al., 2016). More generally, this change in growth patterns towards a "cold type" is in line with the predictions stating that, in a stable environment, individuals should delay their switch to reproduction to maximize fitness (Berrigan and Charnov, 1994; Charnov et al., 2001; Kozłowski, 1996). This would resemble a switch from *r* to *K* strategy (MacArthur and Wilson, 1967; Pianka, 1970) at the population scale. This raises an interesting point. The TSR has been considered as puzzling because it does not correspond to this expected switch from *r* to *K* strategy. Our results suggest that the patterns should be considered as nested: within TSR patterns, individuals at a given temperature over several generations will tend to adopt cold/*K* strategies.

However, changing environment (unstable *i.e.* different ancestral and developmental temperatures) appeared to lead to other types of strategy. The impacts of developmental temperature varied according to the traits (reproduction, growth) and the nature of the thermal change (cooling *vs.* warming) compared to the ancestral temperature. Plasticity of growth and reproduction strategies between treatments sharing ancestral temperature (W_W *vs.* W_C or C_C *vs.* C_W) fitted the TSR patterns as originally defined (Atkinson, 1994) and was higher (wider magnitude of reaction norm) for individuals sharing cold ancestral temperatures (C_W *vs.* C_C) than for individuals sharing warm ones (W_C *vs.* W_W). In addition, growth strategies of crossed treatments appeared more similar to typical pattern of developmental condition ("cold" vs "warm" type) and even more intense than homogeneous treatments sharing the same environment (C_W and W_W; W_C and C_C). Conversely, reproduction strategies appeared more confusing, and may depend more on ancestral and/or developmental conditions. Thus difference between ancestral and developmental temperature still played a role, even after long-term exposure during six generations, expressing the complexity of the evolution of response abilities.

More precisely, individuals from C_W exhibited an extreme warm-type TSR strategy (earliest maturity, fastest growth, smallest adult size) compared to other treatments, representing a high energy investment, but resulting in a low fecundity, the opposite of fitness maximization

(Barnes and Partridge, 2003; Berrigan and Charnov, 1994; Charnov et al., 2001; Charnov and Gillooly, 2004; Kozłowski, 1999; Partridge and Coyne, 1997). This high response ability in this case might be affected by the direction of thermal change (Walczyńska et al., 2015) and could therefore be interpreted as a "plastic overshoot". Plasticity can be negative (Donelson et al., 2018) or even maladaptive, notably when the environment is unpredictable (Bonduriansky et al., 2012; Munday, 2014; Reed et al., 2010). This could be the case for the warming experienced after six generations under cold conditions, which may have been perceived as sudden and unpredictable. In this way, individuals with a cold past may have become more sensitive to warmer temperatures. However, phenotypic plasticity, within and between generations, is a powerful way to cope with rapid environmental change such as climate change (Bonduriansky et al., 2012; Crozier and Hutchings, 2014; Donelson et al., 2018; Ramler et al., 2014; Rummer and Munday, 2017; Walczyńska et al., 2017). If this way should prove insufficient, species could see their fitness threatened, which could be a concern in a global warming context.

Conversely, thermal reaction norm appeared lower in the warm line *i.e.* warm ancestral temperature. Individuals from W_C did not mature latest, as an extreme cold strategy would predict, but after W_W and before C_C individuals, suggesting a mix of the two strategies. This highlights a variation in plasticity of the TSR patterns, pointing to a combination of ancestral (past) and developmental (present) effects in growth and reproduction. It recalls the association of maternal and thermal environment effects observed on rotifers in early stages (Walczyńska et al., 2015) and parental environment in sticklebacks (Shama et al., 2014), strengthening the potential adaptive plasticity of the TSR. We can speculate about the reasons for this low plasticity for individuals from the warm line. This pattern could be due to a lower need for plasticity because individuals were less stressed. According to Jensen's inequality, warming would have a stronger effect (Shama, 2017). Transition from cold to warm treatment would then be more constraining than the other way around. Conversely, low plasticity could demonstrate a loss of response abilities. This last hypothesis is alarming because it implies that populations adapted to a warm environment will struggle to face the environmental variabilities (*e.g.* more thermal fluctuations and more frequent extreme events), that are likely to increase in a climate change context (Pachauri et al., 2014; Stocker et al., 2013).

Finally, some limits should be taken into account before generalizing our results. First, the very high plastic capacities after long-term thermal exposure shown in this study may be due to the eurythermal nature of our study model. The broad thermal tolerance of the medakas (0 – 40 °C; Leaf et al., 2011; Shima and Mitani, 2004; Yamamoto, 1975) means that a change, of 10° from 20 °C to 30 °C is not critical for them. However, a change of a few degrees could have a very strong effect on populations with a narrower thermal range and particularly for stenotherms such as polar or tropical species (Donelson et al., 2016; Munday et al., 2017; Muñoz et al., 2015; Rummer and Munday, 2017). There is a need to conduct the same experiment with other species that have narrow thermal ranges. Second, all the individuals considered in our study were derived from the same parental group F0, but were reared over seven generations at different temperatures. From this viewpoint, our results showed most likely transgenerational plasticity in the evolution of TSR, although our experimental design did not enable us to confirm this hypothesis. Transgenerational effects of warming and cooling could be evidenced using split-brood experiments (Bonduriansky et al., 2012; Donelson et al., 2018). The study of later generations, incorporating genotyping analysis (*e.g.* SNPs) would give more clues to distinguish acclimation from adaptation. Quantitative genetic analysis and appropriate breeding design (Muñoz et al., 2015; Rummer and Munday, 2017) such as crossing families associated with trait monitoring would provide information about the contribution of environmental and parental effects (Bonduriansky et al., 2012; Donelson et al., 2018) and possibly distinction between gender (Shama, 2015; Shama and Wegner, 2014; Zhao et al., 2018; Braun et al., 2013; Shama et al., 2016; Roy et al., 2017). Third, for crossed temperature treatments, eggs were transferred to the new temperature regimes after fecundation, and thus experienced the first few hours in the ancestral temperature. Previous studies showed that developmental plasticity through timing and stage of exposure might impact evolution of the TSR (Walczyńska et al., 2015). The ancestral temperature may thus have played a role in the observed response. However, this was for a very short time period since eggs were placed in the new developmental temperature, assuring larval development under the same environment as the rest of the lifespan. Environmental change during ontogeny (Donelson et al., 2018; Engqvist and Reinhold, 2016; Roy et al., 2017) can have long-term effects and can notably influence physiology, morphology and behaviour of individuals (Marquis et al., 2008). Moreover, transgenerational plasticity depends on life stages (Munday et al., 2017). Walczyńska et al. (2015) state that at least for Rotifera, difference in adult body size leading to TSR patterns is mainly impacted by temperature before hatching and not post-hatching. It would be useful to extend our experiment with thermal change at different stages to test divergence of plasticity (egg, hatching, pre-maturity, post-maturity, late adult).

5. Conclusion

We report evidence that plastic TSR patterns are still present after seven generations of exposure to cold and warm temperatures. However, plasticity in growth and reproduction depended on the thermal history of the populations, with more plastic individuals in the cold populations that in the warm ones. Moreover, individuals with the same ancestral and developmental temperatures tended to adopt "cold" or "slow" strategies (higher L_∞, a lower k and later maturity than those sharing present crossed treatments) after long-term exposure to cold or warm temperatures. To our knowledge, this is the first study to explore the TSR patterns and trade-off between growth and reproduction continuously in a long experiment after multigenerational exposure to temperatures in an aquatic vertebrate. Our findings enhance our understanding of the life-history trait responses to temperature variations, and give us more insight into variation of plasticity in species enduring thermal constraints, which helps to predict responses to climate change. To go a step further, split-brood experiments with difference stages and genotyping analysis would help to distinguish adaptive, developmental and transgenerational effects.

Authors' contributions

M.D. designed the study and A.I. and A.L. collected data. A.L. managed data and performed analyses. A.L. and M.D. wrote the first draft of the manuscript, and all the authors contributed substantially to revisions.

Data accessibility statement

Data supporting the results are availaible and can be found online as supplementary data at https://doi.org/10.1016/j.jtherbio.2019.07.029.

Conflicts of interest

We declare that we have no competing interests.

Funding

This work was supported by grants from the Région Provence-Alpes-Côte-d'Azur and the Agence Française pour la Biodiversité.

Acknowledgements

We especially thank Elsa Muret, the technical team and all those involved in the laboratory experiment for their help in fish rearing. We thank Fanny Colas for her advice and assistance in statistical analysis. We also thank Arnaud Sentis, Manon Helluy, Kurt Villsen and the four anonymous reviewers for their comments, which much improved the article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2019.07.029.

References

Angilletta, M., Dunham, A.E., 2003. The temperature-size rule in ectotherms: simple evolutionary explanations may not Be general. Am. Nat. 162, 332–342. https://doi.org/10.1086/377187.

Angilletta, M., Steury, T.D., Sears, M.W., 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. Integr. Comp. Biol. 44, 498–509. https://doi.org/10.1093/icb/44.6.498.

Angilletta, M., Wilson, R.S., Navas, C.A., James, R.S., 2003. Tradeoffs and the evolution of thermal reaction norms. Trends Ecol. Evol. 18, 234–240. https://doi.org/10.1016/S0169-5347(03)00087-9.

Arendt, J., 2015. Why get big in the cold? Size-fecundity relationships explain the temperature-size rule in a pulmonate snail (Physa). J. Evol. Biol. 28, 169–178. https://doi.org/10.1111/jeb.12554.

Arendt, J.D., 2011. Size-fecundity relationships, growth trajectories, and the temperature-size rule for ectotherms. Evolution 65, 43–51. https://doi.org/10.1111/j.1558-5646.2010.01112.x.

Atkinson, D., 1994. Temperature and organism size-A biological law for ectotherms? Adv. Ecol. Res. 25. https://doi.org/10.1016/S0065-2504 (08)60212-3.

Atkinson, D., Sibly, R.M., 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. Trends Ecol. Evol. 12, 235–239.

Barnes, A.I., Partridge, L., 2003. Costing reproduction. Anim. Behav. 66, 199–204. https://doi.org/10.1006/anbe.2003.2122.

Bartlett, M.S., 1937. Properties of sufficiency and statistical tests. Proc. R. Soc. Lond. Ser A Math. Phys. Sci. 160, 268–282.

Becker, R.A., Chambers, J.M., Wilks, A.R., 1988. The New S Language.

Berrigan, D., Charnov, E.L., 1994. Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. Oikos 70, 474–478. https://doi.org/10.2307/3545787.

Blanckenhorn, W.U., 2015. Investigating yellow dung fly body size evolution in the field: response to climate change? Evolution 69, 2227–2234. https://doi.org/10.1111/evo.12726.

Blanckenhorn, W.U., 2000. Temperature effects on egg size and their fitness consequences in the yellow dung fly *Scathophaga stercoraria*. Evol. Ecol. 14, 627–643. https://doi.org/10.1023/A:1010911017700.

Bolker, B., Skaug, H., Magnusson, A., Nielsen, A., 2012. Getting started with the glmmADMB package. Available at: glmmadmb.r-forge.r-project.org/glmmADMB.pdf.

Bonduriansky, R., Crean, A.J., Day, T., 2012. The implications of nongenetic inheritance for evolution in changing environments. Evol. Appl. 5, 192–201. https://doi.org/10.1111/j.1752-4571.2011.00213.x.

Brans, K.I., Meester, L.D., 2018. City life on fast lanes: urbanization induces an evolutionary shift towards a faster lifestyle in the water flea *Daphnia*. Funct. Ecol. 32, 2225–2240. https://doi.org/10.1111/1365-2435.13184.

Braun, D.C., Patterson, D.A., Reynolds, J.D., 2013. Maternal and environmental influences on egg size and juvenile life-history traits in Pacific salmon. Ecol. Evol. 3, 1727–1740. https://doi.org/10.1002/ece3.555.

Breckels, R.D., Garner, S.R., Neff, B.D., 2013. Rapid evolution in response to increased temperature maintains population viability despite genetic erosion in a tropical ectotherm. Evol. Ecol. 28, 141–155. https://doi.org/10.1007/s10682-013-9668-5.

Bretz, F., Hothorn, T., Westfall, P., Hothorn, T., Westfall, P., 2016. Multiple Comparisons Using R. Chapman and Hall/CRC. https://doi.org/10.1201/9781420010909.

Brown, J.H., Sibly, R.M., 2006. Life-history evolution under a production constraint. Proc. Natl. Acad. Sci. 103, 17595–17599. https://doi.org/10.1073/pnas.0608522103.

Cailliet, G.M., Smith, W.D., Mollet, H.F., Goldman, K.J., 2006. Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. In: Special Issue: Age and Growth of Chondrichthyan Fishes: New Methods, Techniques and Analysis, Developments in Environmental Biology of Fishes. Springer, Dordrecht, pp. 211–228. https://doi.org/10.1007/978-1-4020-5570-6_2.

Charnov, E.L., Gillooly, J.F., 2004. Size and temperature in the evolution of fish life histories. Integr. Comp. Biol. 44, 494–497. https://doi.org/10.1093/icb/44.6.494.

Charnov, E.L., Turner, T.F., Winemiller, K.O., 2001. Reproductive constraints and the evolution of life histories with indeterminate growth. Proc. Natl. Acad. Sci. 98, 9460–9464. https://doi.org/10.1073/pnas.161294498.

Crozier, L.G., Hutchings, J.A., 2014. Plastic and evolutionary responses to climate change in fish. Evol. Appl. 7, 68–87. https://doi.org/10.1111/eva.12135.

Czarnoleski, M., Kramarz, P., Małek, D., Drobniak, S.M., 2017. Genetic components in a thermal developmental plasticity of the beetle *Tribolium castaneum*. J. Therm. Biol. SI Ectotherm.: Perform. 68, 55–62. https://doi.org/10.1016/j.jtherbio.2017.01.015.

Daufresne, M., Lengfellner, K., Sommer, U., 2009. Global warming benefits the small in aquatic ecosystems. Proc. Natl. Acad. Sci. 106, 12788–12793. https://doi.org/10.1073/pnas.0902080106.

Denny, J.S., 1991. Guidelines for Culturing the Japanese Medaka (*Oryzias latipes*).

Donelson, J.M., Salinas, S., Munday, P.L., Shama, L.N.S., 2018. Transgenerational plasticity and climate change experiments: where do we go from here? Glob. Chang. Biol. 24, 13–34. https://doi.org/10.1111/gcb.13903.

Donelson, J.M., Wong, M., Booth, D.J., Munday, P.L., 2016. Transgenerational plasticity of reproduction depends on rate of warming across generations. Evol. Appl. 9, 1072–1081. https://doi.org/10.1111/eva.12386.

Engqvist, L., Reinhold, K., 2016. Adaptive trans-generational phenotypic plasticity and the lack of an experimental control in reciprocal match/mismatch experiments. Method. Ecol. Evol. 7, 1482–1488. https://doi.org/10.1111/2041-210X.12618.

Fabacher, D.L., Little, E.E., 2000. Introduction. In: Ostrander, G.K. (Ed.), The Laboratory Fish, Handbook of Experimental Animals. Academic Press, London, pp. 1–9. https://doi.org/10.1016/B978-012529650-2/50003-2.

Fischer, K., Fiedler, K., 2002. Reaction norms for age and size at maturity in response to temperature: a test of the compound interest hypothesis. Evol. Ecol. 16, 333–349. https://doi.org/10.1023/A:1020271600025.

Forster, J., Hirst, A.G., 2012. The temperature-size rule emerges from ontogenetic differences between growth and development rates. Funct. Ecol. 26, 483–492. https://doi.org/10.1111/j.1365-2435.2011.01958.x.

Forster, J., Hirst, A.G., Atkinson, D., 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. Proc. Natl. Acad. Sci. 109, 19310–19314. https://doi.org/10.1073/pnas.1210460109.

Forster, J., Hirst, A.G., Esteban, G.F., 2013. Achieving temperature-size changes in a unicellular organism. Int. Soc. Microbial. Ecol. J. 7, 28–36. https://doi.org/10.1038/ismej.2012.76.

Fuxjäger, L., Wanzenböck, S., Ringler, E., Wegner, K.M., Ahnelt, H., Shama, L.N.S., 2019. Within-generation and transgenerational plasticity of mate choice in oceanic stickleback under climate change. Philos. Trans. R. Soc. Biol. Sci. 374, 20180183. https://doi.org/10.1098/rstb.2018.0183.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L., Heinsohn, R., 2011. Declining body size: a third universal response to warming? Trends Ecol. Evol. 26, 285–291. https://doi.org/10.1016/j.tree.2011.03.005.

Ghosh, S.M., Testa, N.D., Shingleton, A.W., 2013. Temperature-size rule is mediated by thermal plasticity of critical size in *Drosophila melanogaster*. Proc. R. Soc. Biol. Sci. 280, 20130174. https://doi.org/10.1098/rspb.2013.0174.

Hemmer-Brepson, C., 2013. Effets de la température sur la balance oxydative de vertébrés ectothermes aquatiques à différentes échelles spatio-temporelles et conséquences sur les traits d'histoire de vie . modèle poisson, Aix-Marseille.

Hemmer-Brepson, C., Replumaz, L., Romestaing, C., Voituron, Y., Daufresne, M., 2014. Non-stressful temperature effect on oxidative balance and life history traits in adult fish (*Oryzias latipes*). J. Exp. Biol. 217, 274–282. https://doi.org/10.1242/jeb.096172.

Hirshfield, M.F., 1980. An Experimental analysis of reproductive effort and cost in the Japanese medaka, *Oryzias Latipes*. Ecology 61, 282–292. https://doi.org/10.2307/1935187.

Hirst, A.G., Horne, C.R., Atkinson, D., 2015. Equal temperature–size responses of the sexes are widespread within arthropod species. Proc. R. Soc. Biol. Sci. 282, 20152475. https://doi.org/10.1098/rspb.2015.2475.

Hoefnagel, K.N., Vries, E.H.J, (Lisenka) de, Jongejans, E., Verberk, W.C.E.P., 2018. The temperature-size rule in *Daphnia magna* across different genetic lines and ontogenetic stages: multiple patterns and mechanisms. Ecol. Evol. 8, 3828–3841. https://doi.org/10.1002/ece3.3933.

Honěk, A., 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66, 483–492. https://doi.org/10.2307/3544943.

Horne, C.R., Hirst, A.G., Atkinson, D., 2017. Seasonal body size reductions with warming covary with major body size gradients in arthropod species. Proc. R. Soc. Biol. Sci. 284, 20170238. https://doi.org/10.1098/rspb.2017.0238.

Horne, C.R., Hirst, A.G., Atkinson, D., 2015. Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. Ecol. Lett. 18, 327–335. https://doi.org/10.1111/ele.12413.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50, 346–363. https://doi.org/10.1002/bimj.200810425.

Kaplan, R.H., 1992. Greater maternal investment can decrease offspring survival in the frog Bombina orientalis. Ecology 73, 280–288. https://doi.org/10.2307/1938739.

Kavanagh, K.D., Haugen, T.O., Gregersen, F., Jernvall, J., Vøllestad, L.A., 2010. Contemporary temperature-driven divergence in a Nordic freshwater fish under conditions commonly thought to hinder adaptation. BMC Evol. Biol. 10, 350. https://doi.org/10.1186/1471-2148-10-350.

Kimura, D.K., 1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77, 765–776.

Kindlmann, P., Dixon, A.F.G., Dostálková, I., 2001. Role of ageing and temperature in shaping reaction norms and fecundity functions in insects. J. Evol. Biol. 14, 835–840. https://doi.org/10.1046/j.1420-9101.2001.00323.x.

Kingsolver, J.G., Huey, R.B., 2008. Size, temperature, and fitness: three rules. Evol. Ecol. Res. 10, 251–268.

Kirchen, R.V., West, W.R., 1976. The Japanese Medaka: its Care and Development. Carolina Biological Supply Company.

Kozłowski, J., 1999. Adaptation: a life history perspective. Oikos 86, 185–194. https://doi.org/10.2307/3546437.

Kozłowski, J., 1996. Optimal initial size and adult size of animals: consequences for macroevolution and community structure. Am. Nat. 147, 101–114.

Kozłowski, J., Czarnołęski, M., Dańko, M., 2004. Can optimal resource allocation models explain why ectotherms grow larger in cold? Integrat. Comparat. Biol. 44, 480–493. https://doi.org/10.1093/icb/44.6.480.

Kuparinen, A., Cano, J.M., Loehr, J., Herczeg, G., Gonda, A., Merilä, J., 2011. Fish age at maturation is influenced by temperature independently of growth. Oecologia 167, 435–443. https://doi.org/10.1007/s00442-011-1989-x.

Leaf, R.T., Jiao, Y., Murphy, B.R., Kramer, J.I., Sorensen, K.M., Wooten, V.G., 2011. Life-history characteristics of Japanese medaka *Oryzias latipes*. Copeia 2011, 559–565. https://doi.org/10.1643/CI-09-190.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biography. Princeton, New jersey.

Magnuson, J.J., 1962. An analysis of aggressive behavior, growth, and competition for food and space in medaka (*Oryzias latipes* (pisces, cyprinodontidae)). Can. J. Zool. 40, 313–363. https://doi.org/10.1139/z62-029.

Majdi, N., Traunspurger, W., Fueser, H., Gansfort, B., Laffaille, P., Maire, A., 2019. Effects of a broad range of experimental temperatures on the population growth and body-size of five species of free-living nematodes. J. Therm. Biol. 80, 21–36. https://doi.org/10.1016/j.jtherbio.2018.12.010.

Małek, D., Drobniak, S., Gozdek, A., Pawlik, K., Kramarz, P., 2015. Response of body size and developmental time of *Tribolium castaneum* to constant versus fluctuating thermal conditions. J. Therm. Biol. 51, 110–118. https://doi.org/10.1016/j.jtherbio.2015.04.002.

Marquis, O., Massot, M., Galliard, J.F.L., 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. Ecology 89, 2575–2583. https://doi.org/10.1890/07-1211.1.

Munday, P.L., 2014. Transgenerational acclimation of fishes to climate change and ocean acidification. F1000Prime Rep, vol. 6. https://doi.org/10.12703/P6-99.

Munday, P.L., Donelson, J.M., Domingos, J.A., 2017. Potential for adaptation to climate change in a coral reef fish. Glob. Chang. Biol. 23, 307–317. https://doi.org/10.1111/gcb.13419.

Munday, P.L., Leis, J.M., Lough, J.M., Paris, C.B., Kingsford, M.J., Berumen, M.L., Lambrechts, J., 2009. Climate change and coral reef connectivity. Coral Reefs 28, 379–395. https://doi.org/10.1007/s00338-008-0461-9.

Muñoz, N.J., Farrell, A.P., Heath, J.W., Neff, B.D., 2015. Adaptive potential of a Pacific salmon challenged by climate change. Nat. Clim. Chang. 5, 163–166. https://doi.org/10.1038/nclimate2473.

Nelson, G.A., 2017. Fishmethods: Fishery Science Methods and Models in R.

Ohlberger, J., 2013. Climate warming and ectotherm body size – from individual physiology to community ecology. Funct. Ecol. 27, 991–1001. https://doi.org/10.1111/1365-2435.12098.

Overstreet, R.M., Barnes, S.S., Manning, C.S., Hawkins, W.E., 2000. Chapter 2 - facilities and husbandry (small fish models). In: Ostrander, G.K. (Ed.), The Laboratory Fish, Handbook of Experimental Animals. Academic Press, London, pp. 41–63. https://doi.org/10.1016/B978-012529650-2/50005-6.

Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W., Christ, R., Church, J.A., Clarke, L., Dahe, Q., Dasgupta, P., Dubash, N.K., Edenhofer, O., Elgizouli, I., Field, C.B., Forster, P., Friedlingstein, P., Fuglestvedt, J., Gomez-Echeverri, L., Hallegatte, S., Hegerl, G., Howden, M., Jiang, K., Jimenez Cisneroz, B., Kattsov, V., Lee, H., Mach, K.J., Marotzke, J., Mastrandrea, M.D., Meyer, L., Minx, J., Mulugetta, Y., O'Brien, K., Oppenheimer, M., Pereira, J.J., Pichs-Madruga, R., Plattner, G.-K., Pörtner, H.-O., Power, S.B., Preston, B., Ravindranath, N.H., Reisinger, A., Riahi, K., Rusticucci, M., Scholes, R., Seyboth, K., Sokona, Y., Stavins, R., Stocker, T.F., Tschakert, P., van Vuuren, D., van Ypserle, J.-P., 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 637–669.

Partridge, L., Barrie, B., Barton, N.H., Fowler, K., French, V., 1995. Rapid laboratory evolution of adult life-history traits in *Drosophila melanogaster* in response to temperature. Evolution 49, 538–544. https://doi.org/10.1111/j.1558-5646.1995.tb02285.x.

Partridge, L., Barrie, B., Fowler, K., French, V., 1994. Evolution and development of body size and cell size in *Drosophila melanogaster* in response to temperature. Evolution 48, 1269–1276. https://doi.org/10.2307/2410384.

Partridge, L., Coyne, J.A., 1997. Bergmann's rule in ectotherms: is it adaptive? Evolution 51, 632–635. https://doi.org/10.2307/2411139.

Pérez-Valencia, L.I., Moya-Raygoza, G., 2015. Body size variation of *Diaphorina citri* (Hemiptera: psyllidae) through an elevation gradient. Ann. Entomol. Soc. Am. 72. https://doi.org/10.1093/aesa/sav072.

Pianka, E.R., 1970. On r- and K-Selection. Am. Nat. 104, 592–597.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.C., 2017. nlme: linear and non-linear mixed effects models. R Pack. Vers. 3, 96.

Pörtner, H.O., Farrell, A.P., 2008. Physiology and climate change. Science 322, 690–692. https://doi.org/10.1126/science.1163156.

Quinn, T.J., Deriso, R.B., 1999. Quantitative Fish Dynamics. Oxford University Press.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria URL. https://www.R-project.org/.

Ramler, D., Mitteroecker, P., Shama, L.N.S., Wegner, K.M., Ahnelt, H., 2014. Nonlinear effects of temperature on body form and developmental canalization in the three-spine stickleback. J. Evol. Biol. 27, 497–507. https://doi.org/10.1111/jeb.12311.

Reed, T.E., Waples, R.S., Schindler, D.E., Hard, J.J., Kinnison, M.T., 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. Proc. R. Soc. Biol. Sci. 277, 3391–3400. https://doi.org/10.1098/rspb.2010.0771.

Roff, D., 1992. The Evolution of Life Histories: Theory and Analysis. Chapman and Hall, New York.

Roff, D., 1980. Optimizing development time in a seasonal environment: the 'ups and downs' of clinal variation. Oecologia 45, 202–208. https://doi.org/10.1007/BF00346461.

Roy, A.L., Loughland, I., Seebacher, F., 2017. Differential effects of developmental thermal plasticity across three generations of guppies (*Poecilia reticulata*): canalization and anticipatory matching. Sci. Rep. 7, 4313. https://doi.org/10.1038/s41598-017-03300-z.

Royston, P., 1995. Remark as R94: a remark on algorithm as 181: the W-test for normality. J. Royal Stat. Soc. Ser. C (Appl. Stat.) 44, 547–551. https://doi.org/10.2307/2986146.

Rummer, J.L., Munday, P.L., 2017. Climate change and the evolution of reef fishes: past and future. Fish Fish. 18, 22–39. https://doi.org/10.1111/faf.12164.

Salinas, S., Brown, S.C., Mangel, M., Munch, S.B., 2013. Non-genetic inheritance and changing environments. Non-Genet. Inherit. 1, 38–50.

Schulte, P.M., Healy, T.M., Fangue, N.A., 2011. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. Integr. Comp. Biol. 51, 691–702. https://doi.org/10.1093/icb/icr097.

Sentis, A., Binzer, A., Boukal, D.S., 2017. Temperature-size responses alter food chain persistence across environmental gradients. Ecol. Lett. 20, 852–862. https://doi.org/10.1111/ele.12779.

Shama, L.N.S., 2017. The mean and variance of climate change in the oceans: hidden evolutionary potential under stochastic environmental variability in marine sticklebacks. Sci. Rep. 7, 8889. https://doi.org/10.1038/s41598-017-07140-9.

Shama, L.N.S., 2015. Bet hedging in a warming ocean: predictability of maternal environment shapes offspring size variation in marine sticklebacks. Glob. Chang. Biol. 21, 4387–4400. https://doi.org/10.1111/gcb.13041.

Shama, L.N.S., Mark, F.C., Strobel, A., Lokmer, A., John, U., Mathias Wegner, K., 2016. Transgenerational effects persist down the maternal line in marine sticklebacks: gene expression matches physiology in a warming ocean. Evol. Appl. 9, 1096–1111. https://doi.org/10.1111/eva.12370.

Shama, L.N.S., Strobel, A., Mark, F.C., Wegner, K.M., 2014. Transgenerational plasticity in marine sticklebacks: maternal effects mediate impacts of a warming ocean. Funct. Ecol. 28, 1482–1493. https://doi.org/10.1111/1365-2435.12280.

Shama, L.N.S., Wegner, K.M., 2014. Grandparental effects in marine sticklebacks: transgenerational plasticity across multiple generations. J. Evol. Biol. 27, 2297–2307. https://doi.org/10.1111/jeb.12490.

Shima, A., Mitani, H., 2004. Medaka as a research organism: past, present and future. Mech. Develop. Medaka 121, 599–604. https://doi.org/10.1016/j.mod.2004.03.011.

Sibly, R.M., Atkinson, D., 1994. How rearing temperature affects optimal adult size in ectotherms. Funct. Ecol. 8, 486–493. https://doi.org/10.2307/2390073.

Skaug, H., Fournier, D., Nielsen, A., Magnusson, A., Bolker, B., 2014. glmmADMB: Generalized Linear Mixed Models Using AD Model Builder. R Package. version 0.8. 0.

Stearns, S.C., 1992. The Evolution of Life Histories. Oxford University Press, pp. 249.

Steigenga, M.J., Fischer, K., 2007. Within- and between-generation effects of temperature on life-history traits in a butterfly. J. Therm. Biol. 32, 396–405. https://doi.org/10.1016/j.jtherbio.2007.06.001.

Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, B., Midgley, B.M., 2013. IPCC, 2013: Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Takehana, Y., Uchiyama, S., Matsuda, M., Jeon, S.-R., Sakaizumi, M., 2004. Geographic variation and diversity of the cytochrome b gene in wild populations of medaka (*Oryzias latipes*) from korea and China. Zool. Sci. 21, 483–491. https://doi.org/10.2108/zsj.21.483.

Trip, E.D.L., Clements, K.D., Raubenheimer, D., Choat, J.H., 2014. Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient. J. Anim. Ecol. 83, 866–875. https://doi.org/10.1111/1365-2656.12183.

van der Have, T.M., de Jong, G., 1996. Adult size in ectotherms: temperature effects on growth and differentiation. J. Theor. Biol. 183, 329–340. https://doi.org/10.1006/jtbi.1996.0224.

von Bertalanffy, L., 1960. Fundamental aspects of normal and malignant growth. Princ. Theory Growth 137–259.

von Bertalanffy, L., 1957. Quantitative laws in metabolism and growth. Q. Rev. Biol. 32, 217–231. https://doi.org/10.1086/401873.

Walczyńska, A., Franch-Gras, L., Serra, M., 2017. Empirical evidence for fast temperature-dependent body size evolution in rotifers. Hydrobiologia 796, 191–200. https://doi.org/10.1007/s10750-017-3206-3.

Walczyńska, A., Sobczyk, M., Czarnoleski, M., Kozłowski, J., 2015. The temperature–size rule in a rotifer is determined by the mother and at the egg stage. Evol. Ecol. 29, 525–536. https://doi.org/10.1007/s10682-015-9771-x.

Yamamoto, T., 1975. Medaka (Killifish): Biology and Strains. Yugaku-sha.

Zhao, C., Zhang, L., Shi, D., Ding, J., Yin, D., Sun, J., Zhang, B., Zhang, L., Chang, Y., 2018. Transgenerational effects of ocean warming on the sea urchin *Strongylocentrotus intermedius*. Ecotoxicol. Environ. Saf. 151, 212–219. https://doi.org/10.1016/j.ecoenv.2018.01.014.

Zuur, A.F., Hilbe, J.M., Leno, E.N., 2013. A Beginner's Guide to GLM and GLMM with R: A Frequentist and Bayesian Perspective for Ecologists. Highland Statistics Ltd, Newburgh.