

# Density-dependent consequences of size-selective induced life-history changes to population fitness in medaka (*Oryzias latipes*)

Charlotte Evangelista, Leif Asbjørn Vøllestad, Beatriz Diaz Pauli, and Eric Edeline

**Abstract:** There is an increasing concern about the potential for size-selective harvest to impair population persistence. Yet little is known about the relative contribution of the evolutionary (shifts in life history) and demographic effects (decreased population density and size truncation) of harvesting to changes in fitness. Using medaka (*Oryzias latipes*), we experimentally investigated the fitness consequences of antagonistic size-dependent selection under contrasted levels of density (low versus high) and size structure (uniform versus truncated). The size-dependent selection generated large- and small-breeder lines with fast growth and late maturity versus slow growth and early maturity life histories, respectively. A decrease in density had a positive effect on almost all fitness components, while size truncation only had a positive effect on fish growth. Small-breeder fish grew slower and had a greater probability of reproducing, at least when considering small-sized females. The number of larvae and juveniles did not differ between the two lines. Finally, the positive effect of decreased density on population asymptotic growth rate was less pronounced in small-breeders than in large-breeders of medaka. These findings stress the importance of considering the ramifications of fishing-adapted life history to population persistence in the light of density-dependent population dynamics.

**Résumé :** Les effets potentiellement négatifs de la pêche taille-sélective sur la persistance des populations de poissons sont préoccupants. Pourtant, les effets relatifs de l'évolution (changement d'histoire de vie) et de la démographie (réduction des densités et troncation des tailles corporelles) dans les changements de valeur sélective induits par la pêche restent mal évalués. Nous avons testé expérimentalement chez le médaka (*Oryzias latipes*) les conséquences de la sélection taille-dépendante sur la valeur sélective, et ce à différents niveaux de densité (faible et forte) et de structure en taille (complète ou tronquée). Au préalable, nous avons généré par sélection bi-directionnelle sur la taille deux lignées évolutivement divergentes de médaka caractérisées l'une par une reproduction à une petite taille corporelle (petits reproducteurs), et l'autre par une reproduction à une grande taille corporelle (grands reproducteurs). La diminution de la densité a eu un effet positif sur presque toutes les composantes de la valeur sélective, alors que la troncation des tailles n'a eu d'effet que sur la croissance corporelle. Les individus de la lignée des petits reproducteurs grandissaient moins rapidement et avaient une plus forte probabilité de se reproduire, du moins quand on considérait les femelles de petite taille. Le nombre de larves et de juvéniles était similaire entre les deux lignées. Enfin, l'effet positif de la diminution de densité sur la valeur sélective moyenne était moins prononcé dans la lignée des petits reproducteurs. Ces résultats soulignent l'importance de considérer les répercussions des changements d'histoire de vie induits par la pêche sélective sur la persistance des populations, en particulier dans un contexte de changement densité-dépendant de la dynamique des populations.

## Introduction

Anthropogenic perturbations can have detrimental effects on biodiversity, not solely through the loss of large species (Dirzo et al. 2014; Scheffers et al. 2016; Merckx et al. 2018), but also by altering within-species trait diversity (e.g., morphological, behavioural, and trophic traits; Bolnick et al. 2011; Palkovacs et al. 2012; Mimura et al. 2017). For instance, the five most pervasive anthropogenic threats (i.e., habitat changes, resource over-exploitation, climate change, biological invasion, and pollution) mainly favour small-sized morphological traits within species due to increased mortality of large individuals (Carlson et al. 2007; Hendry et al. 2008; Darimont et al. 2009; Edeline 2016; Sullivan et al. 2017). Such nonrandom mortality has subsequent consequences for popula-

tion dynamics through reduced density and a truncated size structure. In turn, these demographic effects may also impact upon evolutionary processes due to the associated changes in life-history traits. The sustainability of wild populations strongly relies on their capacity to adapt to these nonindependent demographic and evolutionary changes.

Anthropogenic selection on body size is expected to profoundly affect population dynamics, notably due to size-asymmetric competition for resources and energy allocation (Byström and Andersson 2005; Persson and De Roos 2013). Usually, larger individuals dominate in interference competition (Le Boulot Tully and Claessen 2014), while exploitative competition favours small individuals due to their higher energetic efficiency (De Roos et al. 2003). How-

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ever, larger individuals may compensate for their energetic handicap through interference competition and cannibalism, particularly so in gape-size-limited species, such as fish (Persson et al. 2003). Therefore, changes in size structure within populations can alter population dynamics through changes in the strength of ecological interactions such as intercohort competition and cannibalism (De Roos et al. 2003; Rudolf 2012; Bassar et al. 2015). Additionally, the magnitude of these interactions may also be density-dependent (Polis 1981). For instance, populations of guppies (*Poecilia reticulata*) that have a truncated size structure displayed stronger size-dependent competitive abilities (i.e., increased competitive ability with increasing body size) than populations with evenly distributed size structure. However, this asymmetric response was only reported at a high fish density and ultimately influenced individual somatic growth rate (Potter et al. 2018). Predicting how anthropogenic selection impacts the dynamics of harvested populations requires an assessment of these size- and density-dependent processes and how they interact.

Many life-history traits are correlated with body size, and changes in body size can ultimately have profound effects at both the individual and population level (Woodward et al. 2005). Fishing, by usually targeting larger individuals, is predicted to result in evolutionary shifts towards slower somatic growth rates (i.e., smaller body size-at-age) and earlier maturation (Fraser 2013; Heino et al. 2015). Although early maturation may increase the viability of harvested populations because younger individuals have a higher probability of reproducing before being harvested, reproduction at a smaller body size decreases fecundity and offspring quality (Walsh et al. 2006; Uusi-Heikkilä et al. 2015) and may incur increased reproductive mortality (Hutchings, 2005). However, fitness consequences of these evolutionary changes can be counteracted by the phenotypically plastic effects of harvesting. Indeed, increasing resource availability plastically increases somatic growth and reproduction through the release from competition and may thus compensate for the negative effects of size-dependent mortality on fitness components (Law 2000). So far, the relative contribution of shifts in life history, reduced density, and size truncation to fitness components have not been quantified, likely due to the challenge to control each of them in the wild. Laboratory selection experiments are thus needed, as they allow phenotypic plasticity and environmental conditions to be controlled (Heino et al. 2015), as well as specific traits to be targeted under selection (e.g., body size: Conover and Munch 2002; Uusi-Heikkilä et al. 2015).

By combining experimental and matrix population modelling approaches, we investigated how fisheries-induced changes (i.e., life-history shift, decreased density, size truncation) can shape individual fitness components and asymptotic growth of populations. We used medaka (*Oryzias latipes*) from lines previously selected for fast somatic growth and late maturity versus slow somatic growth and early maturity during 10 generations following the size-dependent selection procedure developed by Renneville et al. (2020). This procedure consisted of allowing the smallest or the largest breeders to reproduce and hence obtain two lines with contrasting life histories: the large-breeders (i.e., only large individuals were allowed to reproduce; hereinafter referred to as LB) and the small-breeders (i.e., only small individuals were allowed to reproduce; hereinafter referred to as SB). SB medaka displayed life histories mimicking those of populations exposed to fishing in the wild (i.e., slow growth and early maturity). LB medaka had opposite life histories (i.e., fast growth and late maturity) and mimicked a more natural size selection (Renneville et al. 2020). Here, the two lines were exposed to two contrasting densities (i.e., high versus low) and size structures (i.e., uniform versus truncated where large-sized individuals are absent) during a 4-month laboratory experiment where several fitness components (i.e., growth by length and weight, adult survival, reproduction probability, number of larvae and juveniles) and the asymptotic population growth rate ( $\lambda$ ) were quantified. We predicted that overall fitness

in our experiment would be lower in SB medaka due to their shift towards fishing-like life histories (Walsh et al. 2006). We also predicted that the positive effect of decreased density on fitness would be lower in SB medaka due to their overall lower performance in our experiment, as seen in earlier experiments with these lines (e.g., reduced willingness to forage, lower consumption rate; Diaz Pauli et al. 2019). Finally, we predicted that size truncation would enhance fitness due to the relaxation of interference competition and (or) cannibalism (Bassar et al. 2015), but that this effect would be stronger under high densities.

## Materials and methods

### Size-dependent selection and fish rearing

Native to East Asian countries, the medaka is a small fish species (adult length = 32 mm) that is relatively easy to raise under laboratory conditions and has a short generation time, making it an ideal species for experimental studies (Kinoshita et al. 2009). Individuals originated from two artificial size-selected lines bred under controlled laboratory conditions (temperature: 26 °C, photoperiod: 14 h light : 10 h dark) across 10 generations. Although the protocol developed by Renneville et al. (2020) included a control line (i.e., size-independent selection), we decided not to use this line because our aim was to test whether medaka with opposite life histories differentially respond to changes in density and size truncation. Specifically, large-breeder (LB) and small-breeder (SB) lines were generated by removing small-sized or large-sized individuals, hence allowing only large-sized or small-sized breeders to reproduce, respectively. In each generation, the bidirectional selection was applied on the standard body length ( $SL \pm 1$  mm) at both the family and individual level. At 60 days posthatch (dph), among a total of 20 families per line, only the 10 families with the largest and smallest average SL were retained. At 75 dph, all individuals within each family were measured, and the largest (LB) or the smallest (SB) mature males ( $n = 2$  or 3) and females ( $n = 2$  or 3) were used as breeders for the following generation. In both lines, breeders from different families were paired using pedigree data to minimize genetic drift and inbreeding (mean  $\pm$  SD inbreeding rate at F10: 17.8%  $\pm$  1.2% in LB and 13.8%  $\pm$  1.9% in SB; mean effective population size at F10:  $N_e = 23.2$  in LB and  $N_e = 30.5$  in SB). This selection procedure resulted in keeping, on average, 16% ( $\pm 30\%$  SD) and 8% ( $\pm 6\%$  SD) of fish in the LB and SB, respectively, at each generation. Siblings from a breeding pair were raised in the same tank at constant density (14–17 individuals per 3 L tank) to keep track of pedigrees (Renneville et al. 2020). Fish were fed ad libitum with a mixed diet of dry food and living *Artemia salina* nauplii and (or) *Turbatrix acetii*. The use of identical rearing conditions ensured that observed differences between the two lines were genetic rather than environmental (Conover and Munch 2002) and that these selected lines were evolving in response to size-selective harvesting alone. After seven generations of selection, mature medaka from the SB line were 5.5% shorter in standard length and presented three times higher odds of being mature than their LB conspecifics (Renneville et al. 2020).

### Experimental design

The experiment consisted of a  $2 \times 2 \times 2$  full factorial design with size-selected line (LB and SB) crossed with density (high: Hd; low: Ld) and size structure (uniform: U = small- and large-sized fish present; truncated: T = large-sized fish absent). Each treatment combination was replicated four times. High- and low-density treatments consisted of eight and four fish, respectively, with a 1:1 sex ratio. Hence, densities in our experiment (0.8 and 0.4 fish·L<sup>-1</sup>) were lower than the densities used during the previous generations of selection (6 fish·L<sup>-1</sup>; Renneville et al. 2020) and also biologically appropriate for small fish like medaka (e.g., Potter et al. 2018). The size structure treatment was applied in both lines to assess the response of each line to size truncation induced by

harvesting. Size-truncated structure consisted of only small fish, while uniform size structure consisted of large and small fish in similar proportions and hence mimics the natural population size structure before harvesting. Specifically, on 16 March 2017, fish were anaesthetized with MS-222 (tricaine methanesulfonate), sexed according to secondary sexual characters (Kinoshita et al. 2009), measured for initial standard length ( $SL_i \pm 1$  mm), weighed for initial body mass ( $W_i \pm 1$  mg), and marked to recognize each sex per size category (large-sized female: LF; large-sized male: LM; small-sized female: SF; small-sized male: SM) using a combination of four elastomer colours (Visible Implant Elastomer; Northwest Marine Technology, Shaw Island, Washington, USA). Within each size category (small or large), individuals were chosen to be within a similar range of  $SL_i$  (large  $SL_i$ :  $23 \pm 0.16$  mm SE; small  $SL_i$ :  $19 \pm 0.10$  mm SE). This allowed us to differentiate the effect of size-selection versus the effect of size structure. Females and males were size-matched per size category per line, but large-sized males from the LB line were on average slightly larger than large-sized males from the SB line (refer to online Supplementary material S1<sup>1</sup>).

Two days before the start of the experiment, differences between uniform and truncated distribution indicated a 9% and 7% change in mean standard length in the LB and SB lines, respectively (mean  $\pm$  SE;  $SL_i$  in LB line:  $21.3 \pm 0.18$  mm and  $19.4 \pm 0.22$  mm in uniform and truncated distributions;  $SL_i$  in SB line:  $21.0 \pm 0.26$  mm and  $19.6 \pm 0.15$  mm in uniform and truncated distributions). In addition,  $SL_i$  and  $W_i$  did not significantly differ between the two lines (Tukey post hoc;  $SL_i$ :  $t = -0.13$ , adjusted (adj)  $P = 0.896$ ;  $W_i$ :  $t = 0.92$ , adj  $P = 0.367$ ), nor between density treatments (Tukey post hoc;  $SL_i$ :  $t = -0.09$ , adj  $P = 0.285$ ;  $W_i$ :  $t = -0.42$ , adj  $P = 0.680$ ).

On 18 March 2017, fish from different families were pooled to create 32 artificial populations with minimum intrapopulation inbreeding (mean  $\pm$  SE kinship coefficient =  $0.17 \pm 0.1$  and  $0.23 \pm 0.1$  in LB and SB populations, respectively) and were then introduced into 10 L tanks (30 cm  $\times$  15 cm) connected to a common recirculation system. In each tank, one floating shelter made of wool threads (10 cm length) provided a spawning substrate, and one ball of floating plastic thread provided protection for larvae. The 32 tanks were distributed among the two sides of a three-shelf unit, and fish were maintained under similar laboratory conditions as before, allowing for optimal conditions for growth and development (Kinoshita et al. 2009). During the duration of the experiment, fish were hand-fed with 40 mg of large food pellets (Gemma Micro 300) delivered twice a day. This quantity represented a daily ration of 5% of individual initial body mass calculated from the average weight of all fish at the beginning of the experiment. In addition, 2 mg of small food pellets (Gemma Micro 150) were added daily in each tank to feed the larvae.

For each artificial population ( $n = 32$ ), several demographic components were estimated as proxies for fitness (i.e., growth in length and weight of marked fish, adult survival probability, reproduction probability, recruitment estimated as the number of larvae and juveniles). Except for growth, these fitness components were quantified from count data derived from 25 visual observation events established during 20 March to 20 July 2017 at various intervals (at interval of 2 to 15 days, mean  $\pm$  SD =  $5 \pm 4$  days). Specifically, during each observation, the number of larvae ( $SL < 7$  mm), the number of juveniles ( $SL \geq 7$  mm), and the total number of initial breeders (i.e., marked individuals) were counted, as well as the number of large and small marked females (LF and SF, respectively) carrying eggs attached to their belly. The size limit among the three stages corresponded to visually different morphologies that characterized each category (Kinoshita et al. 2009). Each count was performed by the same observer after the light was turned on between 8:30 pm to 9:30 pm, when the

probability for females to carry eggs was highest. We used a standard time period of 2 min for observing each population to standardize “sampling effort”. Finally, at the end of the experiment, fish in each tank were captured and euthanized with an overdose of MS-222. The recaptured fish (i.e., the marked individuals) were measured for final standard length ( $SL_f \pm 1$  mm), weighed for final body mass ( $W_f \pm 1$  mg), and checked for marks.

### Statistical analyses

All statistical analyses and modelling were performed using R (R Core Team 2019, version 3.5.1). The effects of size-selected line (LB, SB), density (Hd, Ld), and size structure (U, T) on fitness components were tested with linear (LMM; SL and W data) or generalized (GLMM; count data) mixed effects models. LMMs and GLMMs were performed using the nlme (version 3.1-148; Pinheiro et al. 2020) and glmmTMB (version 1.0.1; Brooks et al. 2017) packages, respectively.

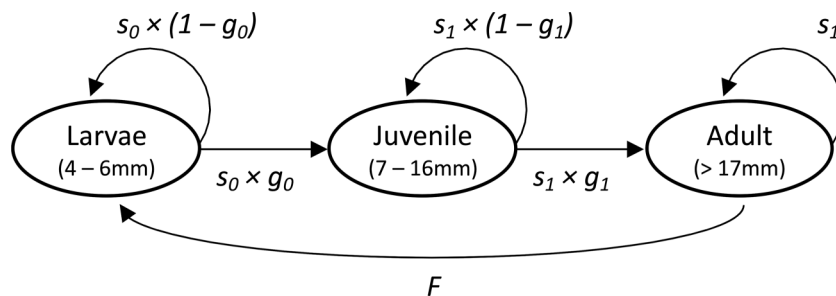
Growth, by length and weight, were modelled using two separate LMMs, using SL or W measured at the start and end of the experiment as dependent variables ( $\log_{10}$ -transformed) and time (in days) as an independent variable. To assess the effects of treatment on length or weight growth, full LMMs were performed including the four-way interactions between time and the three treatments (i.e., Time  $\times$  Line  $\times$  Density  $\times$  Size structure), as well as all lower-order interactions. To ease model convergence and improve parameter estimation, the variable Time was standardized to have a mean of 0 and a standard deviation of 1. The random part of the LMMs accounted for heterogeneous between-tank variance and common within-tank variance using the pdDiag() function from nlme. After visual inspection of the residual plots, LMMs also accounted for residual heterogeneity at different Time  $\times$  Line treatments using the varIdent() function (Zuur et al. 2009).

We used binomial GLMMs with a logit link to explore the effects of experimental treatment on adult survival probability and the probability for a female to carry eggs (hereinafter referred to as reproduction probability), while the number of larvae and juveniles were tested using Poisson GLMMs with a log link. All models included a three-way interaction among treatments to explore whether there was an interaction between density and size structure in both lines. However, due to convergence issues, the GLMM with the number of juveniles only included the interactions Line  $\times$  Density and Line  $\times$  Size structure. The GLMM with reproduction probability as a dependent variable also included the interaction Line  $\times$  Density  $\times$  Size category to discriminate between the probability of large-sized and small-sized females to carry eggs. GLMMs were fitted with “TankID” as a random effect and were run with a first-order autoregressive term (AR1) to account for temporal autocorrelation between each observation event. All GLMMs were checked for overdispersion in the residuals using the DHARMA package (version 0.3.1; Hartig 2020), and residual diagnostics (linearity and heteroscedasticity) were completed visually with the same package.

$P$  values of LMMs were estimated by traditional  $F$  tests, while those from GLMMs were obtained from the car package (version 3.0.8; Fox and Weisberg 2019) using Wald  $\chi^2$  test ( $\chi^2$ ) for mixed effect models. When significant, the interactions were further investigated using post hoc Tukey’s pairwise comparison of the estimate marginal means using the emmeans package (version 1.4.7; Lenth 2020), except in the length and weight growth models (LMMs), where the slopes of Time  $\times$  treatment interactions were analysed using the emtrends() function from the emmeans package.

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0406>.

**Fig. 1.** Life-cycle illustration of medaka (*Oryzias latipes*) characterized by three stages (larvae–juvenile–adult), where  $g_0$  and  $g_1$  are the transition rates from larvae to juvenile and from juvenile to adult, respectively,  $s_2$  is adult survival, and  $F$  is fecundity.



### Population growth model

To explore the effects of the treatments on an integrative fitness measure, we calculated the asymptotic rate of population growth ( $\lambda$ ) as the dominant Eigenvalue of a stage-structured transition matrix  $\mathbf{A}$  (Fig. 1). We considered three stages in  $\mathbf{A}$ , namely larvae (4–6 mm SL), juveniles (7–16 mm SL), and adults ( $\geq 17$  mm SL, which is the size at 50% maturity probability; see Edeline et al. 2016):

$$\mathbf{A} = \begin{pmatrix} s_0 \times (1 - g_0) & 0 & F \\ s_0 \times g_0 & s_1 \times (1 - g_1) & 0 \\ 0 & s_1 \times g_1 & s_1 \end{pmatrix}$$

where  $F$  is adult female fecundity (i.e., number of larvae produced per female per time step), and  $s_x$  and  $g_x$  are stage-specific survival and stage-transition rates per time step, respectively (Fig. 1).

We estimated parameters for  $\mathbf{A}$  using statistical models fit to specifically formatted count and somatic growth data (Caswell 2001). The incubation time at 27 °C averages 11 days (Kinoshita et al. 2009), which imposes an 11-day projection interval in our model. We therefore formatted the count data described above by keeping only data points censored at an 11-day interval. We estimated  $F$  as the ratio between number of larvae at  $t + 1$  and number of females at time  $t$  in a Poisson GLMM (Model 1, Table 1) and mean adult survival rate  $s_1$  from the number of marked adult females alive at  $t$  and  $t + 1$ . Juveniles were assumed to also have survival rate  $s_1$ , while we fixed larval survival  $s_0$  at 0.5. To our knowledge, no data are available from the wild to estimate larval survival in medaka. In the laboratory, in the absence of cannibalism from adults, 90% of larvae survive to age 15 dph, after which survival is even higher (Renneville et al. 2020). Hence, although arbitrary, a 50% larval survival seems to be a reasonable assumption in the presence of cannibalisms from adults.

The larvae-to-juvenile and juvenile-to-adult transitions lasted for more than 11 days, and at each time-step, larvae and juveniles could either change stage at a rate of  $g_0$  and  $g_1$ , respectively, or remain in their stage at a rate of  $1 - g_0$  and  $1 - g_1$ , respectively (conditional on survivals  $s_0$  and  $s_1$ ; Fig. 1). This made it impossible to estimate  $g_0$  and  $g_1$  from count data. Instead, we relied on female somatic growth data from marked medaka. We used average SL at the start and end of the experiment for each sex per size category in each tank ( $n = 80$  sex-size groups) and (i) modelled average female size increment as a function of  $SL_i$ , (ii) simulated growth trajectories and time taken to grow through the larval (4–6 mm) and juvenile stages (7–17 mm), and (iii) computed  $g_x$  as the ratio between the projection interval in our model (11 days) and duration of each stage.

Details of the statistical models used to estimate the  $F$ ,  $s_1$ , and  $g_x$  parameters are provided in Table 1. To gain precision in parameter estimation, we used an exploratory analysis and selected the most parsimonious models by discarding all nonsignificant effects. The exploratory analysis differs from a hypothesis testing approach in

terms of aims, data, and methods (see Statistical analysis above) and should not be used to draw conclusions about the effects of experimental treatments on fitness components. Posterior distributions for  $F$ ,  $s_1$ , and  $g_x$  parameters were obtained using the sim() function (package arm version 1.11.1; Gelman and Su 2020). The approach required first to estimate the vector  $\hat{\beta}$  of the parameters, the unscaled estimation covariance matrix  $\mathbf{V}_\beta$ , and the residual variance  $\hat{\sigma}^2$  by maximum likelihood using the lme4 package. Then the sim function simulated the coefficient vector  $\beta$  and residual standard deviation through repeating:

1. Simulating  $\sigma = \hat{\sigma} \sqrt{(n - k)/X}$ , where  $X$  is a random draw from the  $\chi^2$  distribution with  $n - k$  degrees of freedom ( $k =$  number of model parameters).
2. Given the random draw of  $\sigma$ , simulate  $\beta$  from a multivariate normal distribution with mean  $\hat{\beta}$  and variance matrix  $\sigma^2 \mathbf{V}_\beta$ .

The number of repetitions for these two simulation steps were set to 5000. The resultant posterior parameter distributions were used to propagate the error in the model parameter estimates to the computation of  $\lambda$  from the  $\mathbf{A}$  matrices (obtained using the lambda() function in the package popbio version 2.7; Stubben and Milligan 2007). Specifically,  $s_1$  was always fixed at its mean posterior value, and we used either the posterior distribution of  $F$  with  $g_0$  and  $g_1$  fixed to their mean posterior values or the posterior distributions of  $g_0$  and  $g_1$  with  $F$  fixed to its mean posterior value. This was because the  $F$  and  $g_x$  rates were obtained from different models, and posterior simulations were not directly comparable. This procedure led us to compute eight different distributions for  $\lambda$ , one for each Line-by-Density combination times two different posterior distributions.

## Results

### Fitness components

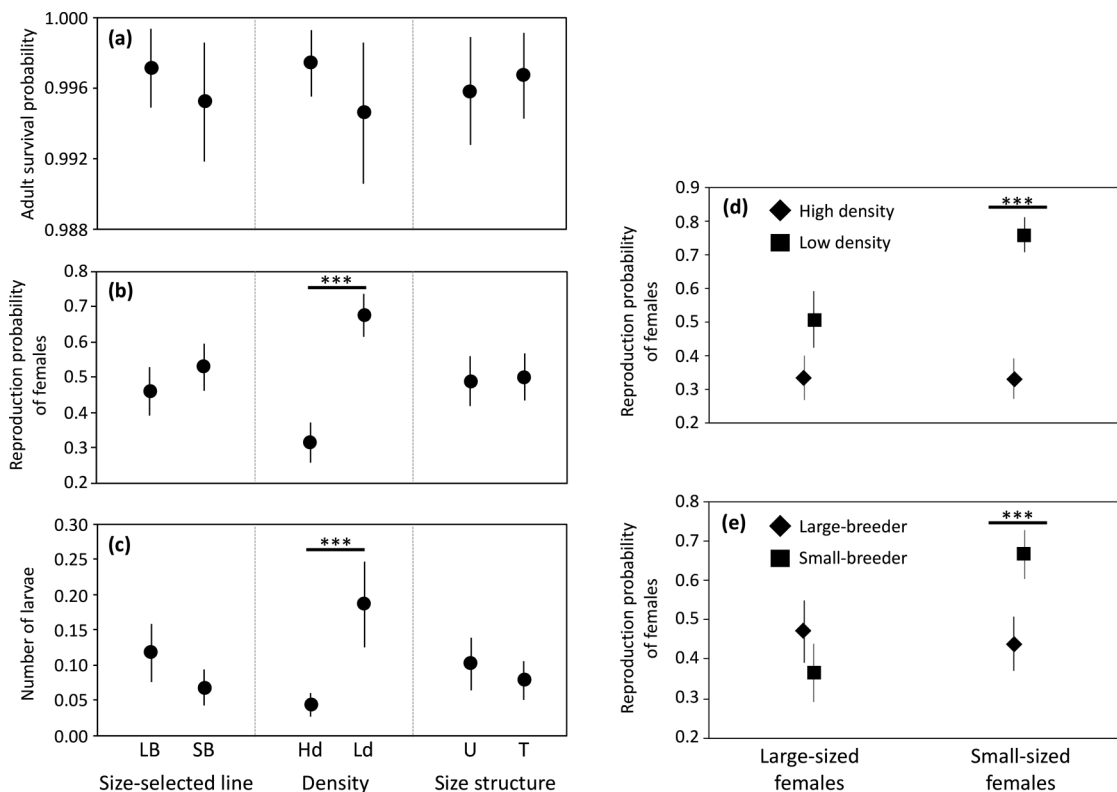
The survival rate of marked adult medaka was relatively high (82%) and did not significantly differ between treatments (Fig. 2a; Table S2.B<sup>1</sup>). SB fish grew 0.71 (95% credible interval: 0.54–0.91) times slower in length than LB medaka, and fish at low densities grew faster than fish at high densities (Figs. 3a–3b; Table S2.A<sup>1</sup>). Fish at low densities were also heavier than fish at high densities, but line had no effect on body weight growth (Figs. 3d–3e; Table S2.A<sup>1</sup>). Medaka from truncated populations grew faster in length and weight than those from uniform populations (Figs. 3c–3f; Table S2.A<sup>1</sup>).

Reproduction probability (estimated here as the probability for a female to carry eggs) was higher at low densities compared with high densities, but did not change with size truncation (Fig. 2b; Table S2.B<sup>1</sup>). Reproduction probability was significantly affected by the interactions Density  $\times$  Size category and Line  $\times$  Size category (Table S2.B<sup>1</sup>). Specifically, small-sized females had higher reproduction probability in low densities compared with high densities (Tukey post hoc:  $t_{1185} = -4.66$ , adj  $P < 0.001$ ; Fig. 2d), while

**Table 1.** Detailed structure of each generalized (GLMMs; Models 1 and 2) and linear (LMM; Model 3) mixed effects models used to estimate the posterior distribution of unknown parameters, intended to parameterize the stage-structure model and calculate the asymptotic population growth rate.

Model	Unknown parameter	Response	A priori component [offset()]	Distribution (link)	Fixed effects
1	Female fecundity, $F$	Number of larvae at $t + 1$ $Nl_i(t + 1) \sim \text{Poisson}(\lambda_i)$ $\log(\lambda_i) = \alpha 1_{\text{Line}[i]} + \alpha 2_{\text{Density}[i]} + \beta_{\text{Tank}[i]} + \log[\text{Nf}(t)]$ , $\beta_{\text{Tank}[i]} \sim N(0, \sigma_\beta^2)$ where $Nl$ is number of larvae, $i$ is individual count, $\text{Nf}$ is number of females, and $\text{Line}[i]$ indicates the line to which observation $i$ belongs (similar for Density and Tank). The four resultant alpha parameters (exponential-transformed) provided $F$ estimates in matrices.	Number of females at $t$	Poisson (ln)	Line $\times$ Density
2	Female survival rate, $s_1$	Proportion of females alive $\text{Nf}(t + 1) \sim \text{Binomial}[\text{Nf}(t), \pi]$ $\log[\pi/(1 - \pi)] = \alpha + \beta_{\text{Day}[i]} + \gamma_{\text{Tank}[i]}$ , $\beta_{\text{Day}[i]} \sim N(0, \sigma_\beta^2)$ , $\gamma_{\text{Tank}[i]} \sim N(0, \sigma_\gamma^2)$ from where the unique alpha (inverse-logit transformed) was used in all matrices for $s_1$ .	—	Binomial	Intercept
3	Duration of the juvenile stage, $g_1$	Female length increment $(SL_j - SL_i) \sim N(\mu_i, \sigma^2)$ $\mu_i = \alpha SL_i + \beta 1_{\text{Line}[i]} + \beta 1_{\text{Density}[i]} + \gamma_{\text{Tank}[i]}$ , $\gamma_{\text{Tank}[i]} \sim N(0, \sigma_\gamma^2)$ where $SL_i$ used in the linear predictor was centred to zero mean. The four resultant beta parameters were used to produce growth trajectories for the four Line $\times$ Density treatments and, from there, the four $g_0$ and $g_1$ in matrices.	—	—	Line $\times$ Density

**Fig. 2.** Predicted probabilities of (a) adult survival, (b) female reproduction (estimated as the number of eggs carried), and (c) larvae number under contrasted size-selected lines (large-breeder (LB) and small-breeder (SB)), densities (high (Hd) and low (Ld)), and size structures (uniform (U) and truncated (T)). Panels (d) and (e) depict the size category-dependent effect (large- versus small-sized females) of densities and size-selected lines on reproduction probability, respectively. \*\*\*,  $P < 0.001$ .



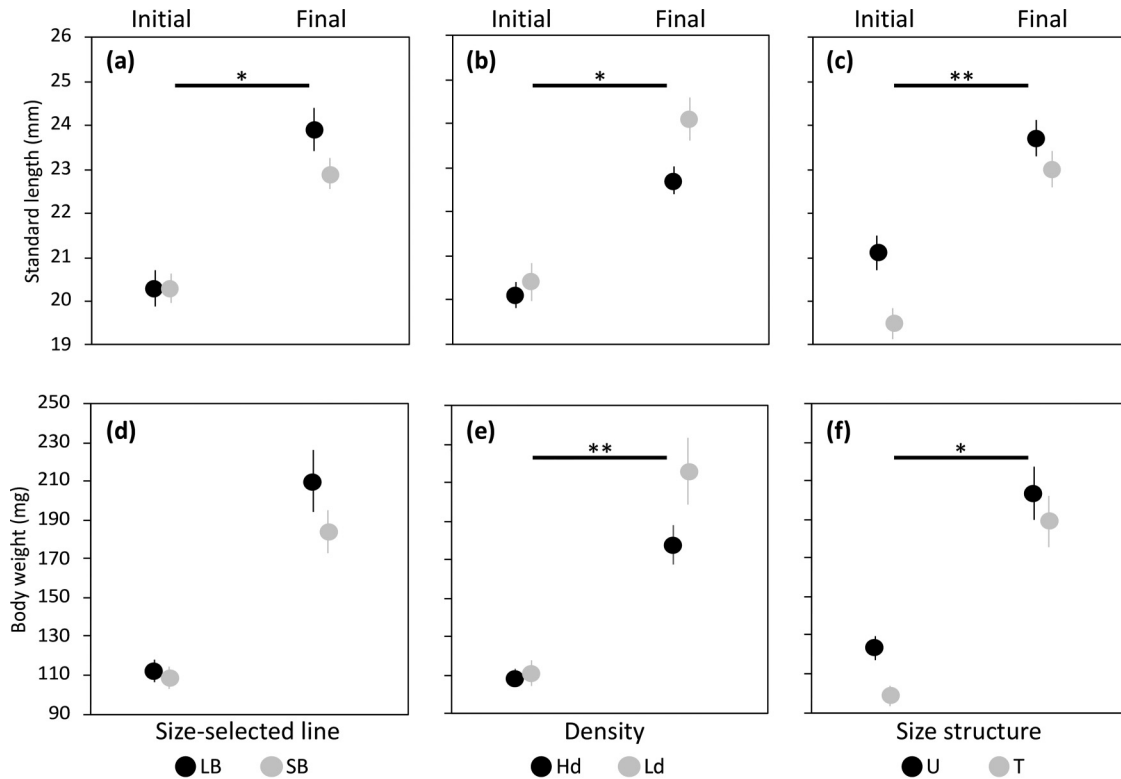
changes in density did not affect the reproduction probability of large-sized females (Tukey post hoc:  $t_{1185} = -1.62$ , adj  $P = 0.106$ ; Fig. 2d). In addition, when considering large-sized medaka, females from the two lines had similar reproduction probability (Tukey post hoc:  $t_{1185} = 0.69$ , adj  $P = 0.329$ ; Fig. 2e), but small-sized females from the SB line had a 1.48 (95% credible interval: 0.77–3.09) greater probability of reproducing compared with those from the LB line (Tukey post hoc:  $t_{1185} = -2.36$ , adj  $P = 0.018$ ; Fig. 2e).

The number of larvae was 3.59 times higher (95% credible interval: 1.42–7.79) at low than at high density but did not differ between lines or size structures (Fig. 2c; Table S2.B<sup>1</sup>). The number of juveniles was not affected by any of the treatments (Table S2.B<sup>1</sup>).

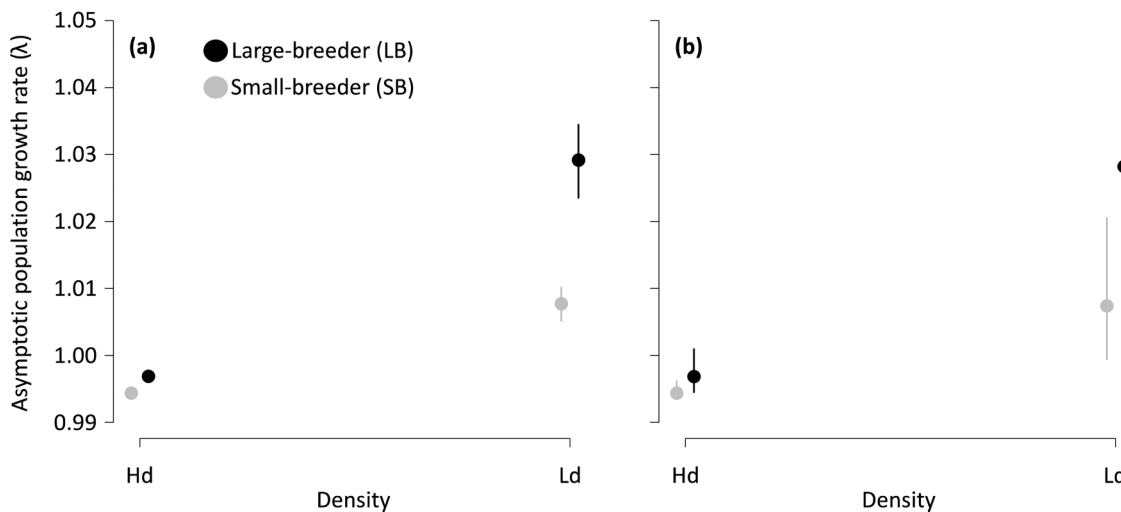
**Population asymptotic growth**

Asymptotic population growth rate ( $\lambda$ ) simulated from both posterior  $g_1$  and  $F$  distributions showed that fecundity generated a

**Fig. 3.** Model estimated standard length (*a–c*) and body weight (*d–f*) of marked medaka (mean  $\pm$  2 SE) measured at the beginning (Initial) and at the end (Final) of the experiment, as well as under contrasted size-selected lines (large-breeder (LB) and small-breeder (SB)), densities (high (Hd) and low (Ld)), and size structure (uniform (U) and truncated (T)). Asterisks indicate significant differences in the slope of time for each treatment (e.g., Time  $\times$  Line): \*\*,  $P < 0.01$ ; \*,  $P < 0.05$ .



**Fig. 4.** Asymptotic population growth rate ( $\lambda$ ) from (a) posterior  $g_1$  (duration of the juvenile stage) and (b) posterior  $F$  (fecundity) for large-breeder (LB, black circles) and small-breeder (SB, grey circles) medaka under high-density (Hd) and low-density (Ld) conditions. Error bars are 95% credible intervals.



larger variability among experimental treatments than somatic growth rate (Fig. 4). Simulations from posterior  $g_1$  indicated that  $\lambda$  was higher at low density than at high density, when growth in length was faster and reproduction was higher (see above) (Fig. 4). Density also modulated the effect of line on  $\lambda$ . Specifically,  $\lambda$  did not differ between LB and SB at high density, and the positive effect of relaxed density on  $\lambda$  was significantly stronger in populations with LB medaka than in those composed of SB medaka (Fig. 4).

## Discussion

Our results show that under standardized laboratory conditions, medaka from the SB line had slower growth in length than LB medaka (Fig. 3a). These individuals also had a higher probability of reproducing, at least when considering small-sized females (Fig. 2d). Reduced population density had an effect on almost all fitness components, while the removal of large-sized individuals (i.e., size truncation) only favoured medaka growth. Specifically,

reproduction probability, the number of larvae produced, as well as growth in both length and weight were higher at low densities compared with high densities. Finally, simulated asymptotic population growth rate ( $\lambda$ ) of medaka showed that the expected increase in population growth due to decreased density was steeper for LB than SB medaka. This suggests that LB populations are more resilient to a reduction in abundance than SB populations, at least under highly controlled experimental conditions.

We confirm that size-dependent selection promotes a life-history shift towards slower growth rate and increased probability of reproducing (Fraser 2013). However, we only found a difference in the probability of producing eggs when we considered the small-sized females, while large-sized females had similar reproduction probabilities in the two lines. Importantly, at the end of the experiment, small-sized females from the LB line were significantly larger than their SB conspecifics, while females were size-matched when the experiment started (Supplement S1<sup>†</sup>). This corroborates the differences in growth (length) between lines, but also indicates that differences in growth were perhaps related to differences in investment into reproduction between LB and SB small-sized females. However, these findings suggest that SB females tended to mature earlier than LB females, as also indicated by the observed lower probabilistic maturation reaction norm of SB medaka during generations F3 to F7 (Renneville et al. 2020). This increased allocation to early reproduction and reduced growth, as well as the observation that the number of larvae and juveniles were similar in the two lines, indicates that other fitness traits were affected in the SB medaka. This agrees with experimental results in *Menidia menidia*, in which selection for small body size reduced larval viability (Walsh et al. 2006). In our experiment, this cost was possibly due to lowered viability of larvae and (or) a decrease in egg quality, since the number of larvae was similar in both lines (despite higher investment in the number of eggs for small-sized SB females). Although our results will require further investigation, we suspect that higher per-offspring energy investment in the LB line is the mechanism explaining differences in egg-to-larvae survival between lines (Rollinson and Hutchings 2013). It is important to keep in mind, however, that lower larval viability represents a cost to early reproduction only in conditions where there is no fishing. When fishing is present, the benefits from early maturation overwhelm this cost.

As expected, a reduced density had a positive effect on various fitness components. Although the probability of reproducing for the large-sized females did not change with density, we found that reduced density favoured the probability of reproducing for the small-sized females. This indicates that release from competition had stronger implications for small- rather than large-sized individuals and also highlights the potential competitive dominance of large-bodied individuals over small-bodied ones. However, our results also show that the removal of large-sized individuals did not favour increased probability of reproducing for small-sized females, highlighting that direct interference competition alone would probably not influence fitness-related characteristics of small-sized fish. It is worth noting that investigating size-asymmetric competition within each tank as in Potter et al. (2018) was not possible here due to the lack of individual size data throughout the experiment. Although we found that the size-structure treatment only played a minor role in structuring fitness components in the populations, we argue that further studies should investigate the complex role of size-dependent asymmetric competition (e.g., following the approach developed by Bassar et al. 2016).

Potential population recovery after a perturbation may be measured as the time needed to recover to its initial population size (Lotze et al. 2011). Here, fish from the SB line had reduced asymptotic population growth under low population densities compared with those from the LB line, thus predicting reduced recovery potential after intensive positive size-dependent selection. In addition, this result may also indicate that the effects of

fishing on traits are likely to remain cryptic if fishing does not strongly decrease densities. This result is consistent with a previous laboratory experiment, which showed that despite life-history evolution induced by size-dependent selection may elevate population persistence under intensive fishing, the long-term sustainability of harvested populations remains uncertain even after fishing is stopped (Uusi-Heikkilä et al. 2015). Similarly, the removal of the largest individuals may lead to population collapse or local extinction in natural environments (Allendorf et al. 2008; Palkovacs et al. 2012). This implies that various compensatory mechanisms (i.e., increased reproductive investment through release from competition) may not always be strong enough to maintain natural populations.

Wild fish populations are challenged by numerous fishing-induced changes, and our study confirms that these changes (i.e., shift towards slow growth, early maturity, and decreased population density) can interact to determine the capacity of harvested populations to rebound. We found that density was the main factor driving direct changes in fitness components, but also that a shift towards fishing-like life histories decreased the sensitivity of population fitness to a decreased density. Thus, these findings may help inform the ongoing debate on the usefulness of so-called “balanced harvesting” (Breen et al. 2016; Gwinn et al. 2015).

#### Data accessibility

Data and scripts that support the findings of this study are available in the Figshare repository: 10.6084/m9.figshare.12619217.

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