Reproductive individuality of clonal fish raised in identical environments and its link to early-life behavioural individuality

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ABSTRACT

Genetic and environmental differences are by far the most studied drivers underlying phenotypic variation. However, a growing number of studies finds among-individual variation that is unexplained by genes or environment. Up to now, it remains an open question whether such seemingly stochastic variation has fitness consequences. To address this question, we performed a tightly controlled long-term life-history experiment with naturally clonal fish (*Poecilia formosa*) separated directly after birth into identical environments. Maintaining highly standardized conditions for 280 days, we first recorded individuals for 10 hours per day over the first 28 days of their lives, characterizing entire early-life behavioural profiles. We then measured the complete reproductive profiles of these individuals over an average of 4.5 successive broods per individual, quantifying in total 2522 offspring from 152 broods. We find that (i) individuals differ consistently in the size of offspring and broods produced over consecutive broods – despite being genetically identical and being raised in identical environments. (ii) These differences are observed even when controlling for trade-offs between brood size, offspring size and reproductive onset, indicating that individuals differ in life-history productivity. (iii) We also find strong early-life behavioural individuality in both activity and feeding pattern, with among-individual differences in feeding being predictive of growth, and consequently reproduction: individuals that consistently spend more time feeding become larger and larger individuals consistently produce larger offspring. Our findings provide experimental evidence that processes unexplained by genetic and environmental differences translate into predictable differences in life-history measures and ultimately reproductive fitness.

49 SIGNIFICANCE STATEMENT

50 According to a long-standing paradigm, genetic and environmental differences are the key
51 drivers underlying variation. More recently, however, this paradigm has been
52 experimentally challenged, finding that substantial anatomical, behavioural and
53 neurobiological among-individual variation emerges in the absence of genetic and
54 environmental differences. But does such variation matter? Here, we show that genetically
55 identical individuals reared in identical environments develop substantial differences in
56 activity and feeding behavior, that individuality in feeding behavior then translates into
57 growth differences, and that ultimately these growth differences affect aspects of the
58 phenotype that probably matter most for fitness: brood size, offspring size and life-history
59 productivity.

INTRODUCTION

Phenotypic differences between individuals from the same species abound throughout the animal kingdom (Bell et al., 2009; Laskowski et al., 2022; Sih et al., 2004), with substantial consequences for fitness, ecology and evolution (Bolnick et al., 2011; Carere & Gherardi, 2013; Ingley & Johnson, 2014; Jolles et al., 2020; Wolf & Weissing, 2012). It is commonly thought that such individuality (if not minor and inconsequential 'noise' or 'idiosyncrasies') is primarily caused by genetic and/or experiential (i.e. environmental) differences. More recently, however, this long-standing paradigm has been experimentally challenged, with accumulating evidence that even genetically identical individuals raised individually and in identical (i.e. highly standardized) environments develop substantial phenotypic differences (Gärtner, 1990; Honegger & de Bivort, 2018; Werkhoven et al., 2021): isogenic fruit flies reared under identical conditions, for example, differ in locomotor handedness and wing-folding, phototaxis, and object-fixated locomotion (Buchanan et al., 2015; Kain et al., 2012; Linneweber et al., 2020); naturally clonal fish reared under identical conditions develop repeatable differences in activity levels, that are already present from the first day of life (Bierbach et al., 2017; Laskowski et al., 2022) (see Freund et al., 2013; Schuett et al., 2011, for related fingings in genetically identical mice and clonal pea aphids).

Such findings are important as they demonstrate that genetic and environmental differences are not the only potent source of variation between individuals, suggesting that factors like pre-birth processes (including epigenetics), development *per se* and/or minor experiential differences may represent other key drivers of phenotypic differences (Ehlman et al., 2022; Hiesinger & Hassan, 2018; Takagi & Benton, 2020; Vogt et al., 2008). Up to

now, however, all recent studies on the emergence of variation in the absence of genetic and environmental differences have focused on characterizing emergent behavioural differences (and their neurobiological underpinnings), but it remains an open question whether or to what extent these differences really matter.

One of the most direct ways to answer this question is to investigate whether phenotypic differences that emerge under genetic and environmental standardization extend to those aspects of the phenotype that directly affect fitness. The goal of the present study is to do exactly this. We performed an experimental study with a live-bearing, naturally clonal freshwater fish, the Amazon molly, *Poecilia formosa*. Directly after birth, we separated genetically identical individuals (N = 34) into identical environments and reared them under highly standardized conditions for 280 days (approx. 10 months). We utilized high-resolution automated long-term tracking of activity and feeding patterns to characterize their early-life behavioural profiles over the first 28 days of their lives (daily recordings for 10 hours at 0.2 s resolution, amounting to a total of 9,520 recording hours and 171.4 million data points) (Ehlman et al., 2023). We then characterized reproductive profiles; recording the onset of reproduction, the size of each brood produced (i.e. the number of offspring per brood; in total, N = 152 broods), and the size of all offspring produced (N = 2522 total offspring), thereby observing 4.5 ± 1.1 broods (mean ± SD) per female (gestation takes approx. 30 days (Farr & Travis, 1986; Snelson et al., 1986). Individual body size was measured weekly.

We focus on three key research questions. First, do genetically identical individuals separated at birth into identical environments develop significant between-individual differences in reproductive traits, i.e. repeatable differences in offspring- or brood size? Second, are between-individual differences in reproductive traits, if present, indicative of differences in (i) life-history productivity, i.e. the ability to produce new biomass (Adriaenssens & Johnsson, 2009; Biro & Stamps, 2008) and/or (ii) how individuals balance the trade-off between brood size vs. offspring size (Charnov et al., 1995; Gomes-Jr & Monteiro, 2007; Lim et al., 2014; Riesch et al., 2012)? Third, are reproductive differences, if present, related to early-life behavioural differences? Such a link could be possible via growth, where behaviour (in particular feeding behavior) could be linked to growth and growth, in turn, to reproductive output (Furness et al., 2021; Gomes-Jr & Monteiro, 2007; Reznick et al., 1996). As an underlying assumption, and as shown previously (Bierbach et al., 2017; Laskowski et al., 2022), we expected repeatable early-life behavioural variation. Whenever appropriate, we focus on repeatability as a key parameter to quantify and test for individuality (e.g. Bell et al., 2009; Biro & Stamps, 2015; Dingemanse & Dochtermann, 2013).

RESULTS

Repeatable differences in early-life behaviour

We find that our genetically identical individuals separated into identical environments on the first day of life, exhibit strong behavioural individuality during the first four weeks of life, both in activity (R = 0.371, 95% CI = [0.329, 0.413]) and feeding behaviour (R = 0.183, 95% CI = [0.145, 0.224]). These repeatable differences even increase when controlling for within-

individual variation caused by individuals growing and becoming older during our observations (adjusted R for activity = 0.571, 95% CI = [0.532, 0.621]; adjusted R for feeding = 0.238, 95% CI = [0.194, 0.285]). Daily activity and feeding behaviour are negatively correlated (estimate = -9.134, CI [-10.550 – -7.719] p-value < 0.0001, R^2 = 0.164, **Tab. 1** in **Suppl. 2**).

Repeatable differences in offspring size, brood size and life-history productivity

We find consistent among-individual differences in both the average size of offspring (**Fig. 1a**, R = 0.396, 95% CI [0.308, 0.484]) and the number of offspring produced (**Fig. 1b**, R = 0.177, 95% CI = [0.117, 0.238]) over consecutive broods. Interestingly, the trade-off between brood size and offspring size explains only little of the variation observed (estimate = -0.013, CI [-0.018, 0.007], p-value < 0.001, partial R^2 = 0.115) (**Fig. 1c**, **Tab. 2** in **Suppl. 2**). And even when controlling for this trade-off, among-individual differences remain: given the same brood size, onset of reproduction, and size at parturition, some individuals consistently produce larger offspring than others (adjusted R for offspring size = 0.134, 95% CI = [0.085, 0.192]), and similarly, while controlling for onset of reproduction, size at parturition, and offspring size, some individuals consistently produce larger broods than others (adjusted R for brood size = 0.077, 95% CI = [0.050, 0.114]). These findings strongly suggest that – next to developing repeatable among-individual differences in offspring size and brood size – our genetically identical individuals, raised individually in highly standardized environments, also differ in life-history productivity.

150 We stress that both offspring- and brood size are the most direct fitness components one
151 can measure, and seemingly small - but repeatable - differences in these traits may have
152 profound long-term consequences. This can be seen, for example, when considering the
153 cumulative number of offspring produced, where even relatively minor individual
154 differences in brood size, when expressed consistently, result in large among-individual
155 differences in total reproductive output (**Fig. 1d**).
156
157
158 *Link between feeding behaviour and offspring size, mediated by growth*
159 Despite no direct link between our two behavioural measures, activity and feeding, and our
160 three reproductive traits, i.e. offspring size (**Fig. 2 a-b**), brood size (**Fig. 2 c-d**), and onset of
161 reproduction (**Fig. 2 e-f**) (**Tab. 3** in **Suppl. 2**), we find an indirect link between one of our
162 behavioural traits and reproduction: fish that spend more time feeding grow to a larger size
163 (estimate = 0.007, CI [0.003, 0.012], p-value = 0.002, partial R^2 = 0.266; **Fig. 3b, Fig. 3d**),
164 and larger fish, in turn, produce larger offspring (**Fig. 3c**; estimate = 0.619, CI [0.299, 0.939],
165 p-value < 0.001, partial R^2 = 0.129). Larger fish also start reproducing later (estimate =
166 55.537, CI [25.189, 85.886], p-value = 0.001, partial R^2 = 0.310; **Fig. 3f**), but there is no
167 effect of reproductive onset on brood size (**Fig. 3e**) (**Tab. 5** in **Suppl. 2**).
168
169 In contrast to feeding behaviour, we find no indirect link between activity and reproduction
170 (**Fig. 3a, Tab. 3** and **Tab. 5** in **Suppl. 2**), nor do we find an effect of our behavioural traits on
171 the growth rate (predicted from fit growth curves; see Methods) (**Tab. 4** in **Suppl. 2**). We
172 note that growth rate and onset of reproduction are negatively correlated: fish that grow

173 faster start reproducing later (estimate = 980.383, CI [235.137, 1725.629], p-value = 0.012,
174 partial R^2 = 0.188), but there is no effect of growth rate on brood- and offspring size (**Tab. 5**
175 in **Suppl. 2**).
176

177 DISCUSSION

178 Employing an experimental 'twin study' approach, we find that genetically identical
179 individuals, raised separately and in highly standardized environments, develop repeatable
180 differences in key reproductive characteristics. In particular, when considering consecutive
181 broods, individuals differ consistently in how many offspring they produce and in how large
182 these offspring are. While we find evidence for a weak trade-off between offspring size and
183 number, repeatable among-individual differences are maintained even when controlling for
184 this tradeoff, as well as for body size and onset of reproduction, providing clear evidence
185 that individuals differ in life-history productivity. While previous studies have provided firm
186 evidence that substantial among-individual variation in anatomical-, behavioural- and
187 neurobiological traits can emerge even in the absence of genetic and environmental
188 differences (Bierbach et al., 2017; Buchanan et al., 2015; Honegger & de Bivort, 2018), the
189 current study builds on and substantially extends these studies by demonstrating that the
190 emerging variation extends to aspects of the phenotype that are directly associated with
191 fitness.
192

193 Interestingly, we find no direct link between early-life behavioural differences and
194 differences in reproductive traits. It is conceivable, that a direct link between early-life
195 behavioural and later-in-life reproductive traits may only become apparent in non-benign

196 and/or more complex environments. To give a concrete example, in our experimental set-
197 up, there are only minimal differential costs/benefits associated with behavioural
198 phenotypes: fish were presented with a stationary food resource, located at a standardized
199 position in tanks with no additional structures. There was no need to search for food and no
200 cost associated with exploiting a stationary food resource. In contrast, in a more naturalistic
201 context, activity might be linked to the ability to find food and the exploitation of a
202 stationary food resource can be risky (Brown, 1992; Verdolin, 2006). That said, it will be
203 interesting to see whether future studies, taking the above and other factors into account,
204 will be able to establish a link between early-life behavioural individuality and reproduction.
205
206 While we do not find a direct link between reproduction and early-life behaviour, we find
207 the size of offspring produced to be linked to early-life feeding behavior: some individuals
208 feed consistently more than others, individuals that feed more grow to a larger predicted
209 final size, and individuals with a larger final size have larger offspring (but not larger broods).
210 The allocation of resources into increasing offspring size, rather than offspring number, may
211 represent an adaptation to environments in which larger offspring have higher fitness, e.g.,
212 resource limitation, competition, or high juvenile mortality (cannibalism or size-dependent
213 predation) (reviewed in Riesch et al., 2012). All of the above factors may apply to our
214 experimental design: during the reproduction period, individuals were fed a standardized
215 amount of food that they shared with a *P. mexicana* male, which we kept in the female's
216 tank as a sperm donor, potentially causing both resource limitation and competition.
217 Furthermore, offspring were removed from the females' tanks directly after parturition,

218 which decreased the risk of cannibalism but may have caused perceived predation from the
219 female's perspective.
220
221 It is intriguing to see that systematic (i.e. repeatable) among-individual differences in key
222 fitness components can emerge even in the absence of genetic and environmental
223 differences. Future work may compare the observed differences in repeatedly expressed
224 reproductive traits to other iteroparous species, taking genetic and/or environmental
225 variation into account, which will give us a better understanding of the magnitude of the
226 observed differences. Furthermore, we will need to evaluate both the causes and
227 consequences of the observed differences. First, all individuals in our study were exposed
228 to one (very specific) environment, and it will be important to investigate whether the
229 observed differences can also be detected in other environments. It will be particularly
230 informative to include predation risk, a key determinant of fitness and major factor shaping
231 life-history trade-offs (Lima & Dill, 1990; Lind & Cresswell, 2005; Reznick & Endler, 1982;
232 Reznick et al., 1996; Walsh & Reznick, 2009), and to investigate, for example, if high-
233 productivity individuals are differently affected by predators than low-productivity
234 individuals. Second, in order to evaluate the consequences of the observed differences in
235 brood- and offspring size, it will be important to investigate whether and to what extent
236 these differences are heritable. Are offspring from mothers with large/small offspring (or
237 large/small brood size) more likely to produce large/small offspring (large/small brood size)
238 themselves? While all our individuals are genetically identical, such inheritance is still
239 conceivable, for example via epigenetic mechanisms (Bocock & Aagaard-Tillery, 2009;
240 Klosin & Lehner, 2016; Kovalchuk, 2012).

241

242 The study of between-individual variation is one of the central themes in ecology and
243 evolution. While such variation – if not minor and inconsequential "noise" – has traditionally
244 been thought to be caused by genetic and environmental differences, evidence is
245 accumulating that even in the absence of such differences, substantial among-individual
246 variation can emerge. Here, we show that such emergent among-individual variation
247 extends to aspects of the phenotype that directly affect fitness. Put differently, we find that
248 the among-individual variation that arises under highly standardized conditions reflects
249 more than just 'idiosyncrasies' or 'noise' – it really matters.

250

251 METHODS

252 *Study species and holding conditions*

253 Amazon mollies used here, were obtained from a stock kept at Humboldt-Universität zu
254 Berlin, (Berlin, Germany). Original stocks were housed in groups of approx. 20-50 fish under
255 standardized conditions: 50-100 liter tanks, 12:12h light:dark cycle, air temperature control
256 (approx. 24±1°C), weekly water changes. Twice a day, fish were fed with powder food (Sera
257 vipan baby). In the stock tanks, Amazon mollies were kept sympatrically with *P. mexicana*
258 males, allowing females to reproduce freely. Before the experiment, we separated potential
259 mothers (originating from the same ancestor) from the stock population in order for them to
260 give birth in individual tanks; this allowed us to track the mother ID (N = 3) of individuals
261 used in this experiment.

262

263 *Early-life behaviour*

264 Individuals were transferred to separate, identical observation tanks (**Fig. 1** in **Suppl. 1**) on
265 the day they were born. Our behavioural observations started the next day, i.e. the first full
266 day of their life. We recorded individuals daily over the first 28 days of their life. Recordings
267 were tracked using the software Biotracker (Mönck et al., 2018), and the movement data
268 obtained from Biotracker (csv-files with xy-coordinates over time) were processed
269 (visualization, calculation of metrics) with a costume repository we developed for this
270 purpose (Stärk et al., 2022) (see **Suppl. 1** for further recording and tracking details). We
271 assessed individual activity as average daily swimming speed (cm/sec). Once a day,
272 individuals were fed with a stationary food resource, a 'food patch', that was positioned at a
273 standardized location in the tank for 2 hours. We assessed the time spent feeding as the
274 amount of time (min), individuals spent in immediate proximity to the food patch (**Suppl. 1**).
275 Food patches were prepared every 2 to 3 days using Sera vipan baby powder food and
276 agar (protocol is provided in **Suppl. 1**).

277

278 *Reproductive profiles*

279 As the Amazon molly is a gynogenetic species, i.e. sperm from one of the parental species
280 (*P. mexicana*, *P. latipinna*) is needed to trigger embryogenesis (but the male's DNA is not
281 incorporated into the offspring's genome (Lamatsch et al., 2005; Schlupp, 2005)), we
282 ensured that females had access to various *P. mexicana* males throughout the reproductive
283 phase.

284

285 We initiated the reproduction phase of the experiment directly after our early-life
286 behavioural observations. We transferred test individuals to individual breeding tanks (11
287 liter, flow-through water system, visual separation between individual tanks) where they
288 remained until the end of the experiment (total observation time per individual is 280 days,
289 approx. 10 months). Breeding tanks were equipped with one *P. mexicana* male as sperm
290 donor, a small plastic pipe (length = 4 cm, diameter = 2 cm), and 'sera biofibres' (a loose
291 bundle of green plastic fibers, structurally comparable to thread algae) as a refuge. Females
292 were swapped between breeding tanks once a week (i.e. males remained in the tank) in a
293 randomized manner to control for a potential tank or male effect. Over the course of the
294 experiment, females had access to approx. 20 different males. Feeding was standardized:
295 twice a day for 5 days a week, fish received 1/64 tsp (up to the age of 70 days) or 1/32 tsp
296 (from the age of 70 to 280 days) of powder food.
297
298 Breeding tanks were checked for offspring daily. Once a female gave birth to a brood, all
299 offspring were photographed and counted. Offspring standard length (i.e. the length from
300 the tip of the snout to the end of the caudal peduncle) was later measured from the photos
301 using ImageJ (Schneider et al., 2012). In total, we recorded 152 broods and measured the
302 size of 2522 offspring from 144 broods (no measurements for 8 broods). Individuals
303 produced on average 4.5 ± 1.1 broods (mean ± SD). We excluded all individuals from our
304 analyses with no or partial reproductive data (*N* = 11 females).
305

306 *Long-term growth*

307 Standard lengths of focal individuals were measured from photos once a week, using
308 ImageJ (Schneider et al., 2012) (34 ± 1 measurements per individual, mean ± SD). We fit
309 individual growth curves using the von Bertalanffy growth model (von Bertalanffy, 1938), a
310 logistic function commonly used to model fish growth. Estimated parameters in this
311 function are the theoretical age when size is zero (t_0), the growth coefficient (K), and the
312 maximum predicted (i.e. asymptotic) size (L_{inf}). For all analyses, we used predicted sizes
313 estimated using individual growth curves rather than raw measurements and characterized
314 individual growth via K and L_{inf} obtained from those individual growth curves.

315

316 *Statistical analysis*

317 *General details*

318 Data were analyzed in R version 4.2.1 (R Core Team, 2022). Most parsimonious LMs (linear
319 models) and LMMs (Linear mixed-effect models; models built using the lme4-package;
320 Bates et al., 2015) were fit via stepwise-backward removal of non-significant predictors.
321 Model assumptions were visually assured using residual- and q-q plots. In the main text, we
322 report estimates and p-values for significant predictors only. The effects of covariates are
323 presented in **Suppl. 2**. Most importantly, individual size at parturition is related to both the
324 number and size of offspring produced (model summaries in **Tab. 3** in **Supp. 2**, figure in
325 **Suppl. 3**); and we found mother ID (*N* = 3) to be related to individual growth and
326 reproductive output (**Suppl. 2**). We therefore included mother ID as a covariate in all
327 models (LMs and LMMs), and individual size at parturition wherever appropriate. In all
328 LMMs, individual ID was included as a random term. Individual size on the first day of life

329 did not affect early-life behavior (**Tab. 1** in **Suppl. 4**), growth (**Tab. 21** in **Suppl. 4**), or
330 reproductive output (**Tab. 31** in **Suppl. 4**); and was therefore not considered during
331 analyses. For significant predictors, we calculated partial R^2 using the *sensemakr*- and
332 *r2glmm*-package (Cinelli et al., 2021; Jaeger, 2017) (for LMs and LMMs, respectively).
333 Complete model summaries of all full (containing all predictors) and final models
334 (containing significant predictors only) are provided in **Suppl. 2**. Model summary tables
335 (including marginal and conditional R^2 following Nakagawa et al., 2017) were built using the
336 package *sjPlot* (Lüdecke, 2022).
337
338 *Repeatabilities*
339 We estimated repeatabilities with 95% CIs (confidence intervals) in two ways: first by
340 building LMMs with only the target variable as response and female ID as random term, but
341 no predictors (i.e. normal repeatability), and then by adding fixed effects to the model,
342 allowing us to estimate the amount of variation caused by consistent between-individual
343 differences while controlling for variation explained by other factors (i.e. adjusted
344 repeatability). The significance of consistent among-individual differences was derived from
345 the 95% CI being distinctly different to 0 (95% CI based on 1000 model simulations) (Hertel
346 et al., 2020).
347
348 To test for 'reproductive individuality', we calculated normal repeatabilities in the size of
349 broods (*N* = 152 broods) and the size of offspring (*N* = 144 broods, average offspring size
350 per brood) over all broods produced. To test for between-individual differences in
351 productivity, we adjusted repeatabilities of both brood- and offspring size for onset, female

352 size at parturition, and mother ID. For the model on brood size, we additionally included
353 offspring size as predictor and vice versa (i.e. we accounted for brood size, offspring size,
354 and onset trade-offs).
355
356 To test for early-life behavioural individuality, we calculated normal repeatabilites for activity
357 (*N* = 941 observations of 34 individuals) and the time spent feeding (LMM with *N* = 932
358 observations of 34 individuals), observed daily over the first 28 days of life. We also
359 adjusted repeatabilities for size and age (week 1-4, categorical variable), i.e. we accounted
360 for variation that was caused by individuals growing and aging over the observation period.
361 We further included a size-age interaction term as predictor (activity was differently affected
362 by size, depending on age). For repeatability calculations, activity was *log*-transformed for
363 normality. We tested if early-life activity (response) and feeding (predictor) are correlated
364 (LMM *N* = 931 observations of 34 individuals).
365
366 *Link between early-life behaviour and reproduction*
367 To test for a behaviour-reproduction link, we built three models with either brood size
368 (LMM with *N* = 152 broods), offspring size (LMM with *N* = 144 broods), or reproductive
369 onset (LM with *N* = 34 individuals) as response. In all models, activity and feeding (averaged
370 over 28 days) were modeled as predictors.
371
372 To test for the link between behaviour and growth, we fit one model on each L_{inf} (LM with *N*
373 = 34 individuals) and K (LM with *N* = 34 individuals), with activity and feeding as predictors
374 (average behaviour over 28 days). When having K as the response, we additionally included

L_{inf} as a covariate to control for the effect L_{inf} has on K; i.e. bigger fish grow slower to their final size L_{inf}, (LM with L_{inf} as response and K as well as mother ID as predictors: intercept [CI] = 6.09 [5.8, 6.4]; estimate of K [CI] = -16.9 [-20.0, -13.8], R^2 = 0.89).

To test for the link between growth and reproduction, we fit a model on each brood size (LMM with *N* = 152 broods), offspring size (LMM with *N* = 144 broods), and onset (LM with *N* = 34 individuals); including K and L_{inf} as predictors and female age at parturition (not in the onset-model) as a covariate.

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FIGURES

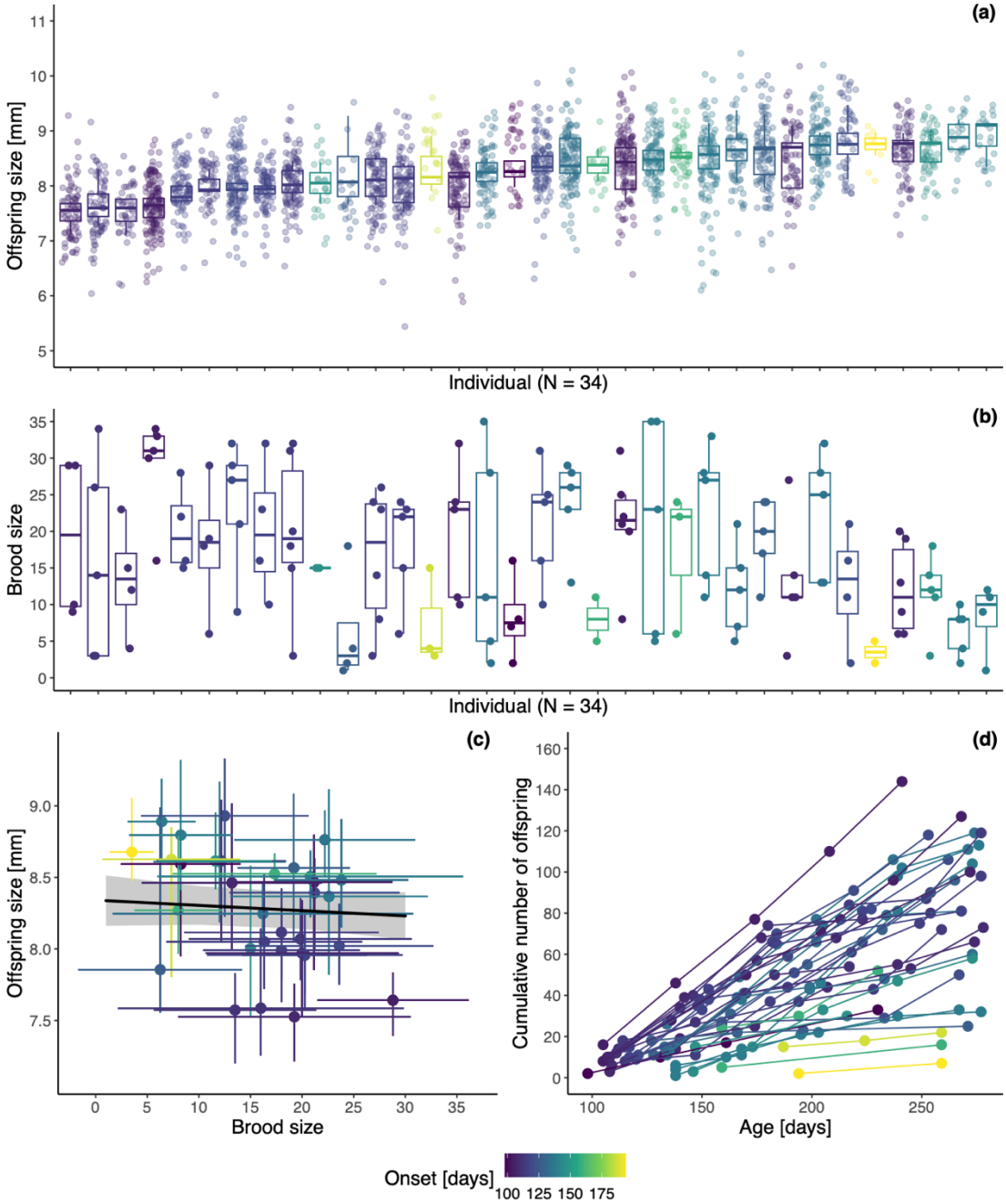

Fig. 1 (a-b) Individuals differ consistently in the size- and number of offspring produced over successive broods; boxplots sorted by median offspring size. (c) The brood size vs. offspring size trade-off explains only very little of the variation; shown are individual averages in brood/offspring size ± standard deviation. (d) Differences in reproductive productivity have profound long-term consequences because reproductive output accumulates over time; shown is the cumulative number of offspring produced by each individual over the first 280 days of life.

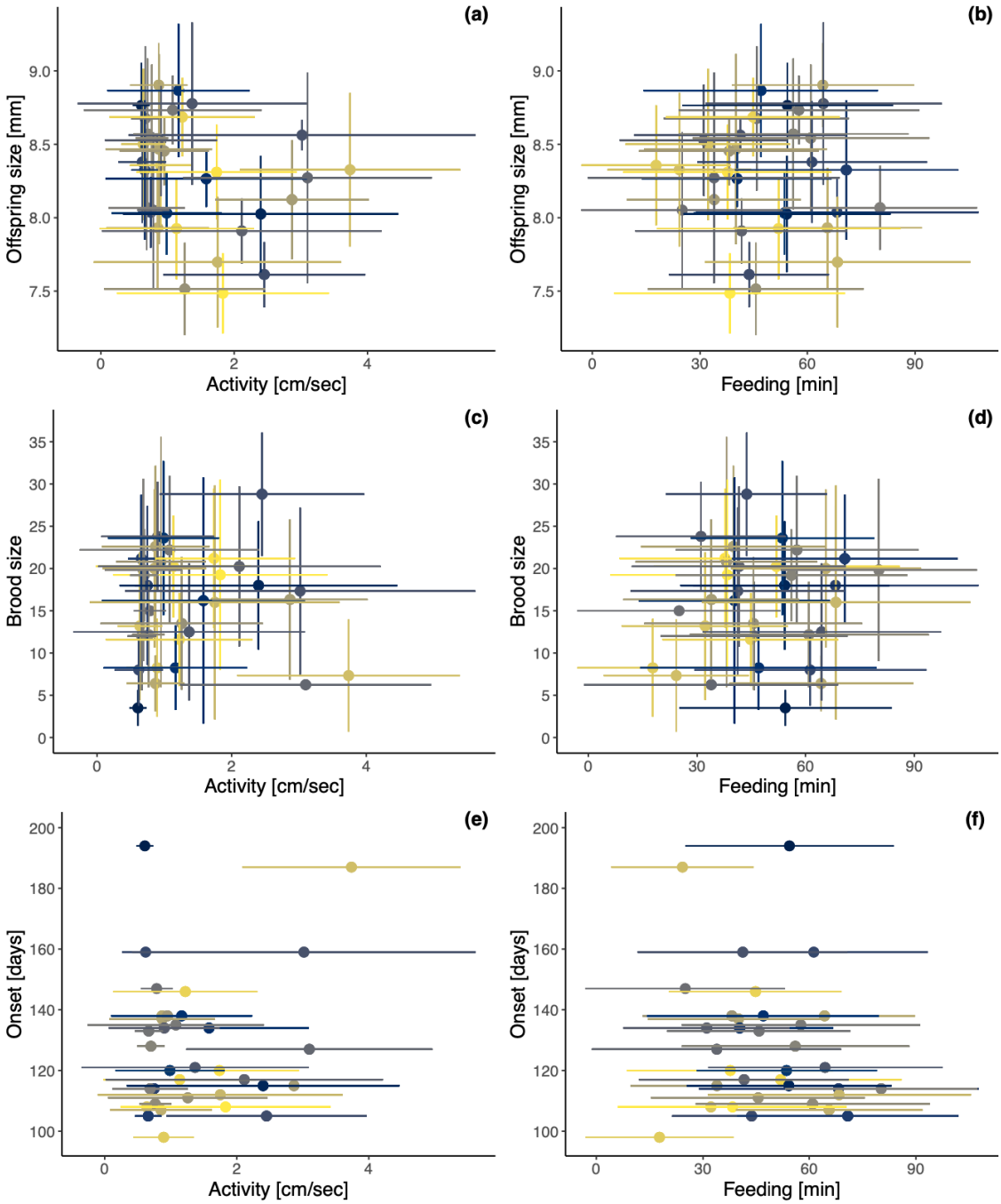

Fig. 2 We find no effect of early-life behaviour (activity and feeding) on offspring size (a-b), brood size (c-d), or onset of reproduction. (e-f) Shown are individual averages (data points) ± standard deviation (error bars); individuals are coloured differently.

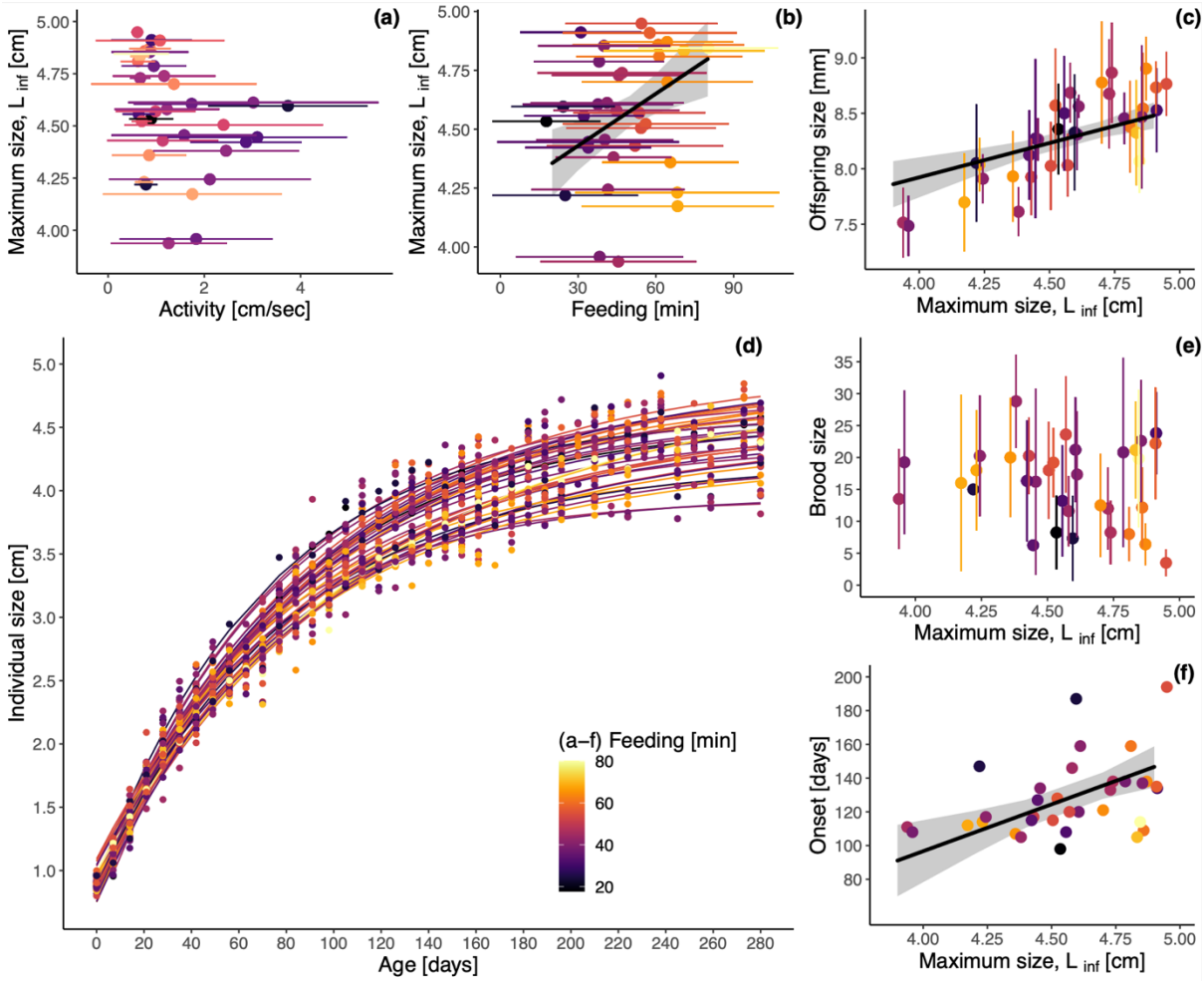

Fig. 3 (a) There is no effect of early-life activity on the final predicted size, L_{inf}, but early-life feeding behaviour and reproductive output are indirectly connected via growth: (b, d) individuals that feed more grow to a larger size, and (c) larger fish produce larger offspring (f). Larger fish also start reproducing later but (e) final size and brood size are not linked. Shown are (b, d) regression lines (black) with 95% CIs, (d), estimates for individual von Bertalanffy growth curves (lines) with raw data (points). (a-c, e) individual averages (points) with standard deviation (error bars).

562 SUPPLEMENT 1

563

564 **Behavioural observations**

565

566 For our early-life behavioural observations, individual observation tanks (**Fig. 1**) were filmed
567 from above with a Basler acA5472 camera (5 frames per second). Activity was recorded over
568 the first 8 hours of each day, followed by a 2-hour feeding. In total, we collected 952
569 recordings of daily activity and feeding behaviour (34 test fish recorded over 28 days).
570 Recordings were tracked using the software Biotracker (Mönck et al., 2018). Quality of
571 tracks was assured via plotting each individual's movement data (i.e., xy-coordinates over
572 time) in 30 min chunks and visually inspecting the trajectory plots for errors.

573

574 To assess individual, daily activity, we used 941 recording days (mean ± SD recording
575 length: 471.7 ± 29.9 min; 11 days were removed from the data due to technical issues).
576 Individual activity was calculated from the xy-coordinates over time in steps of 0.2 sec as
577 the average distance moved (cm) in one second. To calculate how much time individuals
578 spent feeding, we processed feeding recordings of 932 days (mean ± SD recording length
579 = 120.2 ± 11.2 min; 20 recordings were removed due to technical issues). Individual time
580 spent feeding was calculated as the amount of time an individual spent in the 'feeding
581 zone', a 5 x 13 cm large zone surrounding the food patch. For the visualization of
582 movement data and the calculation of metrics (activity, time spent feeding) we a costume
583 repository we developed for this purpose (Stärk et al., 2022).

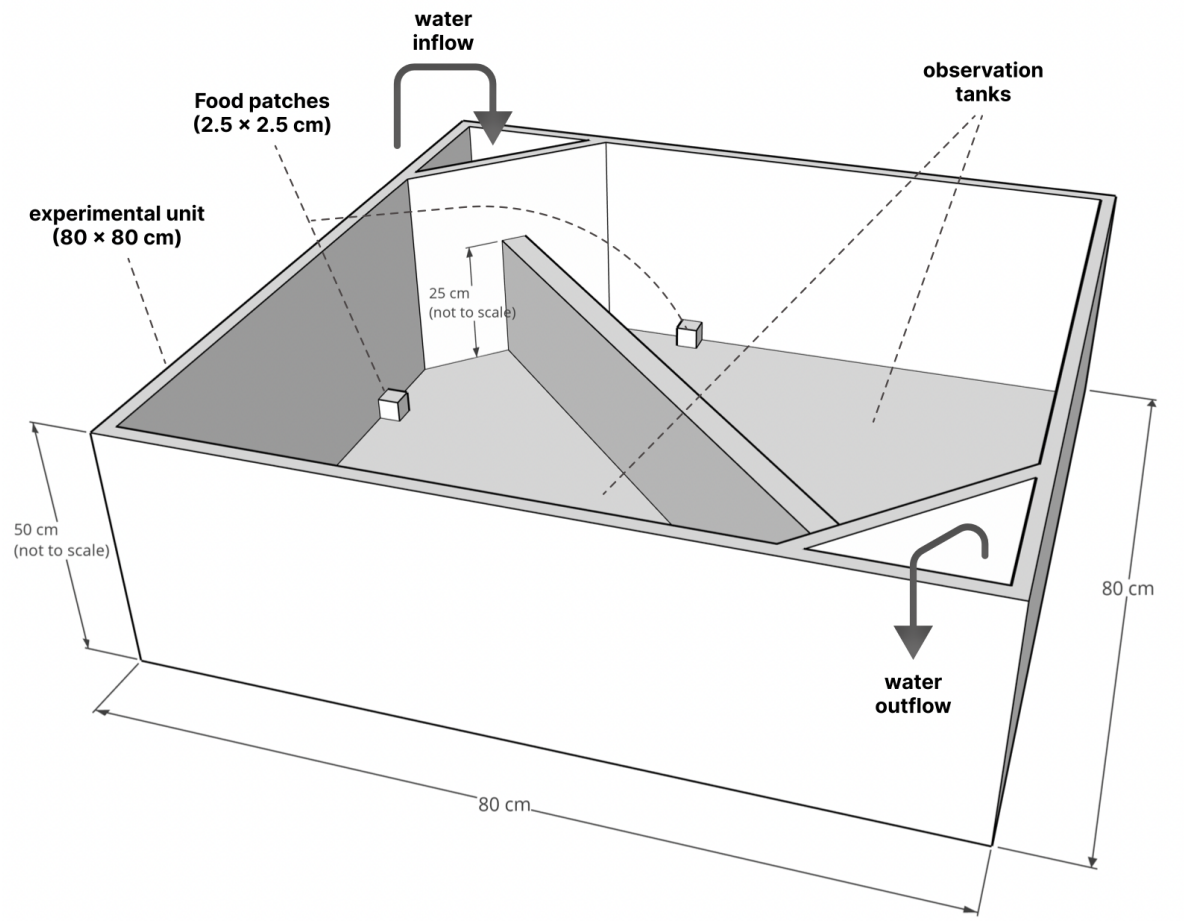

Fig. 1 One experimental unit with 2 observation tanks. Water level in the tanks: 7 cm. Tanks were externally filtered. Food patches were present during the feeding time slots only. There was no visual contact between observation tanks, but tanks were connected via a flow-through water system (24 observation tanks split into 4 flow-through systems).

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602 Food patch preparation

603

604 Ingredients

605 - 0.5g Agar (Bio Agar-Agar, Ruf)

606 - 100 ml tap water

607 - 14 g powder food (Sera vipan baby)

608

609 Materials

610 - One fine scale

611 - One 150 ml beaker

612 - One small pot

613 - One stove plate

614 - One pipette

615 - Food patch cups (max. volume = 2ml)

616

617 Instructions

618 1. Prepare clean and dry food patch forms.

619 2. Weigh the amount of agar needed in a 150 ml beaker.

620 3. Add 100 ml of water.

621 4. Fill the water-agar mixture into a small pot and cook for 2 min at medium heat.

622 5. Remove pot from stove and add powder food, mix thoroughly.

623 6. Let cool down for approx. 5 min at room temperature until agar starts binding.

624 7. Quickly fill the agar-food mixture into the cups using the pipette.

625 8. Let the food patches harden in the fridge for approx. 10 min without a lid.

626 9. Store food patches in a container with a lid (e.g., petri dishes) in the fridge until

627 further proceeding (can be stored for at least 4 days when stored at 4°C).

628

629 Notes:

630 The protocol can be modified regarding the amount of food or agar added. Adding more

631 agar will give the mixture a firmer texture. Using less agar is not advised. The amount of

agar used here is the least amount possible (resulting in a very soft texture) in order to allow juvenile fish to feed on the food patches. The amount of food can be both decreased and increased allowing for variations in food quality; food variations may require adjustments in the amount of agar used.

SUPPLEMENT 2

Tab.1 Full (left) and final (right) models testing if early-life feeding behaviour and activity are correlated.

Response		Full model			Final model		
	Predictors	*Estimate*	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Feeding [min]	Intercept	55.554	48.433 – 62.675	-	60.734	55.675 – 65.792	-
	Activity [cm/sec]	-9.222	-10.644 – -7.800	**<0.001**	-9.134	-10.550 – -7.719	**<0.001**
	Mother ID [m2]	3.103	-11.814 – 18.020	0.088	-	-	-
	Mother ID [m3]	10.495	0.907 – 20.084		-	-	-
	Random Effects						
	σ^2	721.68			721.69		
	τ_{00}	150.82 Test fish ID			165.52 Test fish ID		
	ICC	0.17			0.19		
	N	34 Test fish ID			34 Test fish ID		
	Observations	931			931		
	Marginal R^2 / Conditional R^2	0.174 / 0.317			0.164 / 0.320		

Tab. 2 Full (left) and final (right) models testing for an offspring size vs. brood size trade-off.

		Full model			Final mode		
Response	*Predictors*	*Estimate*	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Offspring size (brood average, mm)	Intercept	5.083	4.238 – 5.927	-	4.466	3.827 – 5.104	-
	Brood size	-0.011	-0.018 – -0.005	<0.001	-0.013	-0.018 – -0.007	<0.001
	Onset [days]	-0.002	-0.006 – 0.002	0.335	-	-	-
	Size at parturition [cm]	0.919	0.730 – 1.108	<0.001	0.988	0.830 – 1.146	<0.001
	Mother ID [m2]	-0.038	-0.273 – 0.196	0.061	-	-	-
	Mother ID [m3]	-0.197	-0.359 – -0.035		-	-	-
	Random Effects						
	σ^2	0.10			0.10		
	τ_{00}	0.01 Test fish ID			0.01 Test fish ID		
	ICC	0.10			0.13		
	N	34 Test fish ID			34 Test fish ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.580 / 0.623			0.545 / 0.602		

Tab. 3 Full (left) and final (right) models testing if early-life behaviour (activity, feeding) predicts reproduction (brood size, offspring size, onset).

		Full model			Final model		
Response	*Predictors*	*Estimate*	*CI*	*P-value*	*Estimate*	*CI*	*P-value*
Brood size	Intercept	-15.029	-35.583 – 5.524	-	-19898	-39.823 – 0.027	-
	Activity [cm/sec]	-2.317	-4.881 – 0.248	0.082	-	-	-
	Feeding [min]	-0.071	-0.207 – 0.066	0.312	-	-	-
	Size at parturition [cm]	8.002	3.307 – 12.697	0.001	7820	3.157 – 12.484	0.001
	Mother ID [m2]	6.108	0.048 – 12.169	<0.001	4324	-1.608 – 10.256	<0.001
	Mother ID [m3]	10.208	5.706 – 14.710		8444	4.353 – 12.535	
	Random Effects						
	σ^2	70.72			70.53		
	τ_{00}	7.54 Test fish ID			10.07 Test fish ID		
	ICC	0.10			0.12		
	N	34 Test fish ID			34 Test fish ID		
	Observations	152			152		
	Marginal R^2 / Conditional R^2	0.160 / 0.241			0.138 / 0.246		
Offspring size (brood average, mm)	Intercept	5.168	4.359 – 5.978	-	5.147	4.366 – 5.928	-
	Activity [cm/sec]	-0.047	-0.149 – 0.056	0.369	-	-	-
	Feeding [min]	0.002	-0.004 – 0.007	0.513	-	-	-
	Size at parturition [cm]	0.791	0.607 – 0.975	<0.001	0.804	0.622 – 0.987	<0.001
	Mother ID [m2]	-0.058	-0.305 – 0.190	0.018	-0.119	-0.356 – 0.118	<0.001
	Mother ID [m3]	-0.265	-0.446 – -0.084		-0.270	-0.434 – -0.107	
	Random Effects						
	σ^2	0.10			0.10		
	τ_{00}	0.01 Test fish ID			0.02 Test fish ID		
	ICC	0.12			0.14		
	N	34 Test fish ID			34 Test fish ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.552 / 0.607			0.539 / 0.605		
Onset of reproduction [days]	Intercept	126.473	94.420 – 158.526	-	133.786	123.545 – 144.027	-
	Activity [cm/sec]	4.000	-6.139 – 14.138	0.426	-	-	-
	Feeding [min]	0.072	-0.458 – 0.602	0.784	-	-	-
	Mother ID [m2]	15.777	-9.037 – 40.590	0.004	19.964	-1.760 – 41.689	0.002
	Mother ID [m3]	-19.908	-35.944 – -3.872		-17.411	-31.434 – -3.387	
	Observations	34			34		
	R^2 / R^2 adjusted	0.341 / 0.250			0.326 / 0.282		

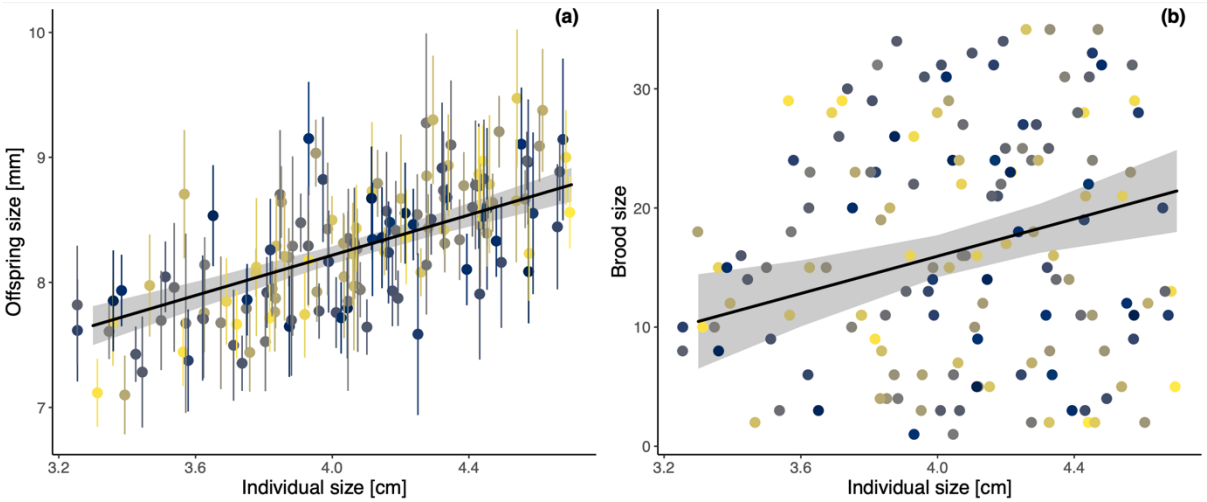
Tab. 4 Full (left) and final (right) models testing for an effect of early-life behaviour on the maximum predicted size (L_{inf}) and growth rate (K) of individuals.

		Full model			Final model		
Response	*Predictors*	*Estimates*	*CI*	*P-value*	*Estimates*	*CI*	*P-value*
L_{inf} [cm]	Intercept	4.465	4.159 – 4.771	-	4.375	4.141 – 4.608	-
	Activity [cm/sec]	-0.045	-0.141 – 0.052	0.354	-	-	-
	Feeding [min]	0.006	0.001 – 0.011	0.015	0.007	0.003 – 0.012	0.002
	Mother ID [m2]	0.144	-0.093 – 0.380	<0.001	0.098	-0.116 – 0.313	<0.001
	Mother ID [m3]	-0.349	-0.502 – -0.196		-0.378	-0.517 – -0.239	
	Observations	34			34		
	R^2 / R^2 adjusted	0.592 / 0.535			0.579 / 0.537		
K	Intercept	0.296	0.247 – 0.344	-	0.305	0.263 – 0.346	-
	Activity [cm/sec]	0.001	-0.001 – 0.004	0.326	-	-	-
	Feeding [min]	0.000	-0.000 – 0.000	0.963	-	-	-
	L_{inf} [cm]	-0.046	-0.056 – -0.035	<0.001	-0.047	-0.056 – -0.039	<0.001
	Mother ID [m2]	0.004	-0.003 – 0.010	<0.001	0.005	-0.001 – 0.011	<0.001
	Mother ID [m3]	-0.019	-0.024 – -0.013		-0.018	-0.023 – -0.014	
	Observations	34			34		
	R^2/ R^2 adjusted	0.814 / 0.781			0.807 / 0.788		

Tab 5 Full (left) and final (right) models testing if von Bertalanffy growth parameters (the growth rate K and maximum predicted size L_{inf}) predict reproduction (brood size, offspring size, onset of reproduction).

		Full model			Final model		
Response	*Predictors*	*Estimates*	*CI*	*P-value*	*Estimates*	*CI*	*P-value*
Brood size	Intercept	43.171	-71.768 – 158.110	-	7.187	1.217 – 13.157	-
	L_{inf} [cm]	-4.576	-23.302 – 14.151	0.630	-	-	-
	K	-173.702	-530.501 – 183.096	0.338	-	-	-
	Age at parturition [weeks]	0.205	0.015 – 0.394	0.035	0.215	0.026 – 0.404	0.026
	Mother ID [m2]	5.630	-0.429 – 11.690	0.111	5.085	-0.828 – 10.999	0.011
	Mother ID [m3]	3.808	-4.004 – 11.620		5.875	2.167 – 9.583	
	Random Effects						
	σ^2	73.73			73.90		
	τ_{00}	8.36 Test fish ID			9.32 Test fish ID		
	ICC	0.10			0.11		
	N	34 Test fish ID			34 Test fish ID		
	Observations	152			152		
	Marginal R^2 / Conditional R^2	0.120 / 0.210			0.105 / 0.206		
Offspring size (brood average, mm)	Intercept	5.739	1.240 – 10.239	-	4.808	3.310 – 6.307	-
	L_{inf} [cm]	0.475	-0.257 – 1.206	0.170	0.619	0.299 – 0.939	<0.001
	K	-3.076	-17.062 – 10.909	0.638	-	-	-
	Age at parturition [weeks]	0.029	0.022 – 0.037	<0.001	0.030	0.022 – 0.037	<0.001
	Mother ID [m2]	-0.081	-0.318 – 0.155	0.026	-0.096	-0.320 – 0.128	<0.001
	Mother ID [m3]	-0.385	-0.689 – -0.080		-0.329	-0.497 – -0.162	
	Random Effects						
	σ^2	0.10			0.10		
	τ_{00}	0.01 Test fish ID			0.01 Test fish ID		
	ICC	0.12			0.11		
	N	34 Test fish ID			34 Test fish ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.568 / 0.618			0.570 / 0.616		
Onset of repro-duction [days]	Intercept	-141.259	-595.812 – 313.294	-	-204.285	-383.856 – -24.714	-
	L_{inf} [cm]	45.090	-29.090 – 119.270	0.224	55.537	25.189 – 85.886	0.001
	K	768.659	-631.930 – 2169.249	0.271	980.383	235.137 – 1725.629	0.012
	Mother ID [m2]	15.631	-7.523 – 38.785	0.393	-	-	-
	Mother ID [m3]	-0.368	-31.794 – 31.058		-	-	-
	Observations	34			34		
	R^2 / R^2 adjusted	0.360 / 0.271			0.317 / 0.273		

SUPPLEMENT 3



Suppl. 3 Female size is positively correlated with (a) offspring size (shown is average offspring size per brood ± SD) and (b) brood size. Data points are coloured by individuals.

SUPPLEMENT 4

Tab. 1 Full (left) and final (right) models testing if size on the first day of life predicts early-life behavior.

		Full model			Final model		
Response	*Predictors*	*Estimates*	*CI*	*P-value*	*Estimates*	*CI*	*P-value*
Activity [cm/sec]	Intercept	1.546	-1.112 – 4.204	-	0.996	0.577 – 1.416	-
	Size at birth [cm]	-0.656	-3.786 – 2.475	0.672	-	-	-
	Mother ID [m2]	1.210	0.301 – 2.118	0.025	1.188	0.298 – 2.077	0.011
	Mother ID [m3]	0.595	-0.079 – 1.269		0.524	-0.050 – 1.098	0.072
	Observations	34			34		
	R^2 / R^2 adjusted	0.218 / 0.139			0.213 / 0.162		
Feeding [min]	(Intercept)	10.888	-38.316 – 60.093	-	48.058	42.847 – 53.268	-
	Size at birth [cm]	42.305	-15.642 – 100.252	0.146	-	-	-
	Mother ID [m2]	-9.241	-26.064 – 7.581	0.454	-	-	-
	Mother ID [m3]	1.021	-11.450 – 13.493		-	-	-
	Observations	34			34		
	R^2 / R^2 adjusted	0.151 / 0.066			0.000 / 0.000		

Tab. 2 Full (left) and final (right) models testing if size on the first day of life predicts reproductive output.

		Full model			Final model		
Response	*Predictors*	*Estimates*	*CI*	*P-value*	*Estimates*	*CI*	*P-value*
Brood size	(Intercept)	-1.708	-18.716 – 15.300	-	7.187	1.217 – 13.157	-
	Size at birth [cm]	10.904	-8.548 – 30.356	0.270	-	-	-
	Age at parturition [weeks]	0.208	0.019 – 0.398	0.031	0.215	0.026 – 0.404	0.027
	Mother ID [m2]	4.675	-1.168 – 10.518	0.086	5.085	-0.828 – 10.999	0.011
	Mother ID [m3]	4.561	0.254 – 8.868		5.875	2.167 – 9.583	
	Random Effects						
	σ^2	74.06			73.90		
	τ_{00}	8.19 Test fish ID			9.32 Test fish ID		
	ICC	0.10			0.11		
	N	34 Test fish ID			34 Test fish ID		
	Observations	152			152		
	Marginal R^2 / Conditional R^2	0.116 / 0.204			0.105 / 0.206		
Offspring size (brood average, mm)	Intercept	8.036	7.306 – 8.766	-	7.685	7.448 – 7.921	-
	Size at birth [cm]	-0.431	-1.276 – 0.414	0.315	-	-	-
	Age at parturition [weeks]	0.031	0.024 – 0.038	<0.001	0.031	0.024 – 0.038	<0.001
	Mother ID [m2]	-0.035	-0.288 – 0.218	<0.001	-0.053	-0.307 – 0.201	<0.001
	Mother ID [m3]	-0.462	-0.649 – -0.276		-0.514	-0.674 – -0.353	
	Random Effects						
	σ^2	0.10			0.10		
	τ_{00}	0.02 Test fish ID			0.02 Test fish ID		
	ICC	0.18			0.19		
	N	34 Test fish ID			34 Test fish ID		
	Observations	144			144		
	Marginal R^2 / Conditional R^2	0.525 / 0.612			0.519 / 0.612		

Tab. 3 Full (left) and final (right) models testing if size on the first day of life predicts the growth rate K and predicted final size L_{inf}.

		Full model			Final model		
Response	*Predictors*	*Estimates*	*CI*	*P-value*	*Estimates*	*CI*	*P-value*
L_{inf}	Intercept	4.171	3.473 – 4.870	-	4.716	4.602 – 4.831	-
	Size at birth [cm]	0.650	-0.172 – 1.473	0.117	-	-	-
	Mother ID [m2]	0.019	-0.220 – 0.258	<0.001	0.041	-0.202 – 0.284	<0.001
	Mother ID [m3]	-0.407	-0.584 – -0.230		-0.337	-0.493 – -0.180	
	Observations	34			34		
	R2 / R^2 adjusted	0.472 / 0.419			0.426 / 0.389		
K	Intercept	0.309	0.268 – 0.350	-	0.305	0.263 – 0.346	-
	L_{inf}	-0.045	-0.054 – -0.036	<0.001	-0.047	-0.056 – -0.039	<0.001
	Size at birth [cm]	-0.017	-0.037 – 0.004	0.107	-	-	-
	Mother ID [m2]	0.006	-0.000 – 0.011	<0.001	0.005	-0.001 – 0.011	<0.001
	Mother ID [m3]	-0.016	-0.021 – -0.010		-0.018	-0.023 – -0.014	
	Observations	34			34		
	R2 / R^2 adjusted	0.824 / 0.799			0.807 / 0.788		