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Contact CEH NORA team at
noraceh@ceh.ac.uk

Fitness consequences of early life conditions and maternal size effects in a freshwater top predator

Yngvild Vindenes^{*a}, Øystein Langangen^a, Ian J. Winfield^b and L.
Asbjørn Vøllestad^a

^aCentre for Ecological and Evolutionary Synthesis (CEES),
Department of Biosciences, University of Oslo, Oslo, Norway

^bLake Ecosystems Group, Centre for Ecology & Hydrology,
Lancaster, U.K.

Running headline: Fitness consequences of early life impacts

Summary

1. Conditions experienced in early life stages can be an important determinant of individual life histories. In fish, environmental conditions are known to affect early survival and growth, but recent studies have also emphasized maternal effects mediated by size or age. However, the relative sensitivity of

*yngvild.vindenes@ibv.uio.no

the mean fitness (population growth rate λ) to different early life impacts remain largely unexplored.

2. Using a female-based integral projection model (IPM) parameterised from unique long-term demographic data for pike (*Esox lucius*), we evaluated the relative fitness consequences of different early life impacts, including i) maternal effects of length on egg weight, potentially affecting offspring (first year) survival, and ii) effects of temperature on offspring growth and survival. Of the seven vital rates defining the model, offspring survival could not be directly estimated and four scenarios were defined for this rate.
3. Elasticity analyses of the IPM were performed to calculate i) the total contribution from different lengths to the elasticity of λ to the projection kernel, and ii) the elasticity of λ to underlying variables of female current length, female offspring length at age 1, and temperature. These elasticities were decomposed into contributions from different vital rates across length.
4. Egg weight increased with female length, as expected, but the effect leveled off for the largest females. However, λ was largely insensitive to this effect, even when egg weight was assumed to have a strong effect on offspring survival. In contrast, λ was sensitive to early temperature conditions through growth and survival. Among mature females, the total elasticity of λ to the projection kernel generally increased with length. The results were robust to a wide range of assumptions.
5. These results suggest that environmental conditions experienced in early life represent a more important driver of mean population growth and fitness of

pike than maternal effects of size on offspring survival. We discuss two general mechanisms underlying the weak influence of this maternal effect, suggesting that these may be general for long-lived and highly fecund fishes. This model and results are relevant for management of long-lived top-predators, including many commercially important fish species.

Keywords

Cohort effects, demographic heterogeneity, delayed life history effects, environmental impacts, individual heterogeneity, silver spoon effects, trait structure.

1 Introduction

2 The phenotype and vital rates of adult life history stages are often shaped by
3 conditions experienced in early life (Lindström, 1999; Beckerman et al., 2002).
4 Young individuals often go through critical processes of ontogenetic development
5 and growth that may be sensitive to external conditions. Individual differences in
6 life history may therefore arise from varying environmental conditions and ma-
7 ternal effects experienced in early life, and can have profound impacts on pop-
8 ulation growth, fitness, and other demographic characteristics at the population
9 level (Coulson et al., 2001; Gaillard et al., 2003; Benton et al., 2006; Vindenes and
10 Langangen, 2015). For size-structured organisms, lasting individual differences in
11 somatic growth rates can potentially generate large differences in survival and fe-
12 cundity over the lifetime, although growth is also influenced by factors at later
13 life stages (De Roos et al., 2003; Monaghan, 2008; Vincenzi et al., 2014). Organ-

14 isms can sometimes compensate for a bad start by increasing growth in later life
15 stages (if environmental conditions improve), but a number of fitness costs are
16 still linked to poor initial growth conditions (Metcalfé and Monaghan, 2001). In
17 fish, mortality tends to be very high for the smallest individuals, partly due to
18 size-dependent predation (Bailey and Houde, 1989), leading to a strong selection
19 pressure for rapid early growth.

20 In addition to impacts of environmental conditions on early growth and sur-
21 vival, recent studies have also emphasized the role of maternal effects in the recruit-
22 ment and population growth of fish, that are associated with female body size and
23 age (Green, 2008; Arlinghaus et al., 2010; Venturelli et al., 2010; Marshall et al.,
24 2011; Hixon et al., 2014). There are several mechanisms through which female size
25 can influence the contribution to recruitment (Brooks et al., 1997; Kamler, 2005).
26 First, in some species large females have been found to produce a larger number
27 of eggs relative to their body mass (Hixon et al., 2014). Second, large females tend
28 to invest more energy per egg, leading to larger larvae with increased swimming
29 performance and resistance to starvation (Wright and Shoemith, 1988; Kamler,
30 1992; Kotakorpi et al., 2013; Green, 2008). The effect of egg size on early survival
31 may not always be positive, however, and may depend on other factors like spatial
32 location, temperature, or time of hatching (Kamler, 1992; Robertsen et al., 2012).
33 Third, large females sometimes spawn at different times and locations, which could
34 increase offspring survival through improved environmental conditions and timing
35 of food availability (Hixon et al., 2014). Maternal effects may also depend on past
36 environmental conditions experienced by the female, such as temperature or re-
37 source levels (Monaghan, 2008). For example, in some fish species egg size has been
38 found to decrease as a plastic response to temperature conditions experienced by

39 the mother prior to spawning, when the eggs are developed (Kamler, 1992; Green,
40 2008).

41 Traditional fishery management assumes that females of different sizes con-
42 tribute equally to recruitment relative to their biomass, so that the population's
43 size structure can be ignored and population growth predicted by the spawning
44 stock biomass alone. However, if large females contribute relatively more than small
45 ones, failing to account for the population's size structure could lead to biased es-
46 timates of recruitment and population growth (Hixon et al., 2014). Some studies
47 have considered and included such maternal size effects in fish (Arlinghaus et al.,
48 2010; Venturelli et al., 2010), but few have evaluated their relative impacts on
49 population growth compared to other factors in the life history. Moreover, earlier
50 studies have focused mainly on the reproductive potential of the population (such
51 as the total egg number produced), but fitness and population growth also depend
52 on other parts of the life history besides reproduction, in particular survival and
53 growth. Depending on the life history of the species, the mean fitness will be more
54 sensitive to certain vital rates and certain life history stages than others (Roff,
55 1996; Caswell, 2001).

56 Evaluating the fitness consequences of early life conditions with lasting effects
57 on the life history requires a model framework that can account for individual het-
58 erogeneity. Integral projection models (IPM) are ideally suited for this purpose,
59 as dynamic changes over the lifetime, for instance in a trait like body size, can be
60 combined with latent individual differences through a static state variable (Vin-
61 denes and Langangen, 2015). For instance, in a recent study on roe deer (*Capreolus*
62 *capreolus*) Plard et al. (2015) used an IPM to evaluate the fitness consequences
63 of timing of birth within season. Early-born offspring were found to be heavier

64 as adults, and had a higher reproductive value (Plard et al., 2015). IPMs are the
65 continuous-state version of matrix models, and are constructed from four main
66 vital rate functions describing how survival, reproduction, state transitions, and
67 initial state distributions in offspring depend on underlying state variables (East-
68 erling et al., 2000; Ellner and Rees, 2006; Rees et al., 2014). These main vital
69 rate functions may in turn be composed of other underlying functions. The many
70 analytical advantages of matrix models (Caswell, 2001) also apply to IPMs (Ellner
71 and Rees, 2006).

72 In this study we extend and analyse an IPM for a population of pike (*Esox*
73 *lucius*) from Windermere, U. K., to evaluate the relative fitness impacts of un-
74 derlying variables via different parts of the life history, as well as to compare
75 the total contribution to population growth from females of different lengths. The
76 model includes an effect of maternal length on egg weight, potentially affecting off-
77 spring survival. Pike is a large and relatively long-lived top predator in freshwater
78 ecosystems across the northern hemisphere (Craig, 2008). It has an iteroparous life
79 history, spawning in spring, preferably on vegetation (Billard, 1996). Temperature
80 is an important determinant of growth and recruitment (Kipling, 1983; Paxton
81 et al., 2009; Casselman, 1996; Rypel, 2012), and is also associated with other vital
82 rates (Vindenes et al., 2014). Some studies have reported a positive effect of female
83 body size on egg size (Billard, 1996; Kotakorpi et al., 2013). Kotakorpi et al. (2013)
84 also reported a positive effect of female length on larval dry weight, as well as on
85 larval survival times under starvation, indicating that offspring from larger eggs
86 have an increased survival probability especially in poor environmental conditions.
87 Maternal size does not seem to have a lasting influence on somatic growth rate in
88 pike, as initial size differences after hatching have been found to level off rapidly

89 over time (Giles et al., 1986).

90 Recently, Vindenes et al. (2014) constructed a temperature-dependent IPM
91 for this population to evaluate the demographic consequences of climate warming,
92 and found contrasting effects on different vital rates at different body lengths. This
93 model was then extended to include individual heterogeneity in somatic growth and
94 survival, as differences in size at age 1 tend to persist (Vindenes and Langangen,
95 2015). In the current study we extend this model to include maternal effects of
96 body length on egg weight, potentially affecting offspring survival.

97 **Materials and methods**

98 **STUDY SYSTEM AND DATA**

99 The study population is located in the glacial lake of Windermere, U. K. (54°22' N,
100 2°56' W; altitude 39 m). Scientific monitoring of the pike population was initiated
101 in 1944, and a review of the study system and data collection methods is given by
102 Le Cren (2001). Data on pike and other major fish populations have been collected,
103 as well as on the abiotic and biotic environment. The main environmental driver
104 considered in this study is the annual mean surface temperature T (measured in
105 Celsius degrees, referred to as temperature; see Appendix A for more details). The
106 average temperature over the study period was about 10.5°C.

107 Three pike data sets were used in this study, to estimate i) somatic growth
108 and offspring length distribution at age 1 (7909 females, 1944-1992), ii) fecundity
109 and egg weight (3696 females, 1963-2003), and iii) survival probability (3992 in-
110 dividuals of both sexes, 1954-1995). The first two data sets are derived from data
111 gathered in a scientific long-term monitoring programme with gillnet sampling in

112 winter (Frost and Kipling, 1959; Le Cren, 2001; Edeline et al., 2007), whereas the
113 survival data were gathered from a capture mark recapture study with sampling
114 also in spring (Kipling and Le Cren, 1984). Somatic growth occurs mainly in the
115 summer months, and in the model we assume that no mortality or growth occurs
116 in the winter months between sampling and spawning (see Fig. A.1, Appendix A).
117 Ovarian development in female pike in Windermere occurs mainly between Octo-
118 ber and March, and spawning occurs from March-May (Frost and Kipling, 1967).
119 The number of offspring (age 1 individuals) may depend on environmental con-
120 ditions both in the spawning year (affecting offspring survival) and the preceding
121 year (affecting fecundity and egg weight, hence offspring survival).

122 In the gillnet sampling, captured pike were measured for body length (fork
123 length, cm), weighed (kg), and sexed, and opercular bones were removed for age
124 and length back-calculation following a method validated for Windermere (Frost
125 and Kipling, 1959). Since 1963, data on female reproductive investment were also
126 collected, including gonad weight (g) and the number of oocytes (referred to here as
127 “eggs”) estimated from counting of a 1 g sample of the gonads (Frost and Kipling,
128 1967). The average egg weight was calculated as the gonad weight divided by the
129 estimated number of eggs (Frost and Kipling, 1967). The number of spawned eggs
130 will generally be slightly lower than this estimate, because some of the oocytes
131 do not ovulate (Billard, 1996). Since the data sampling period overlaps with the
132 egg development in females, it is important to account for capture month in the
133 regression analyses for fecundity and egg weight. The probability of maturity was
134 defined based on a study of Frost and Kipling (1967) where smaller pike were also
135 captured, reporting that most female pike in Windermere become mature at age
136 2, at a mean length of ~ 41.5 cm, ranging from 31 cm to 49.8 cm.

137 CONSTRUCTING THE IPM

138 The model is female-based, assuming a pre-breeding census so that offspring are
139 counted at age 1 (see Table 1 for an overview of the main variables and vital rates).
140 The state variables are current female length x (cm), female offspring length at age
141 1 y (cm), current temperature T ($^{\circ}\text{C}$), and previous temperature T^* ($^{\circ}\text{C}$). Offspring
142 length reflects initial growth differences and is therefore a useful state variable for
143 describing lasting effects of early growth through the life history (Vindenes and
144 Langangen, 2015). For each female in the population, the state variable offspring
145 length y refers to the length of that female at age 1, a measure that remains
146 constant over the lifetime. The vital rates of fecundity (egg number) and egg weight
147 may depend on temperature of the previous year, T^* , when eggs are developed in
148 the female, whereas other vital rates may depend on the current temperature, i.e.
149 during the spawning year (see Appendix A for a detailed description of timing
150 of events in the life history). When temperature is assumed to be constant, as in
151 the elasticity analyses of this study, the current and previous temperature are the
152 same.

153 The four main vital rate functions in the IPM are (notation here includes state
154 variables found to be significant in the results) i) survival probability $s(x, y, T)$, ii)
155 the distribution of next year's length $g(x'; x, y, T)$, a truncated lognormal distri-
156 bution with mean $\mu_G(x, y, T)$ and variance $\sigma_G^2(x)$, describing growth from length
157 x to length $x' \geq x$ next year, iii) the offspring number $b(x, T, T^*)$, describing the
158 number of female offspring at age 1 produced by a female of length x (see fur-
159 ther details in next section), and iv) the distribution of offspring lengths $f(y' : T)$
160 (a lognormal distribution with mean $\mu_{G_1}(T)$ and variance $\sigma_{G_1}^2$) determining the

161 length y' of an offspring as it enters the population next year at age 1.

162 Together, these main vital rate functions define the projection kernel, describing
163 the expected changes in the population structure (distribution of the traits x and
164 y) over time (Easterling et al., 2000). Here, the projection kernel is given by

$$K(x', y'; x, y, T, T^*) = s(x, y, T)g(x'; x, y, T)\delta(y' - y) + b(x, T, T^*)f(y'; T)\delta(y' - x'),$$

165 where $\delta(y' - y)$ is a Dirac delta function included to keep each individual's off-
166 spring length constant over time, while $\delta(y' - x')$ similarly ensures that for an
167 offspring at age 1 the state variables of current length and offspring length have
168 the same value (Vindenes and Langanen, 2015). The projection kernel can be
169 analysed using matrix model methods (eigen analysis; Caswell, 2001; Ellner and
170 Rees, 2006) to obtain the expected long-term population growth rate λ (a measure
171 of average fitness; Caswell, 2001), the joint stable trait distribution $u(x, y)$ (scaled
172 so that $\int \int u(x, y) dx dy = 1$), and the reproductive value $v(x, y)$ (scaled here so
173 that $\int \int v(x, y) u(x, y) dx dy = 1$). These outputs all depend on temperature. Nu-
174 merical calculation of model parameters was done by discretizing the projection
175 kernel (after the vital rates are defined as continuous functions) and applying ma-
176 trix modeling methods on the resulting high-dimensional projection matrix (see
177 details in Appendix A).

178 UNDERLYING FUNCTIONS OF OFFSPRING NUMBER

179 The number of 1 year old female offspring produced by a female in a given year is
180 influenced by many underlying factors. Here we considered the female's probability

181 of maturity $p_m(x)$, fecundity (egg number) $m(x)$, and the offspring survival proba-
182 bility during the first year $s_O(w, T)$. The latter may depend on the female's current
183 length and the previous temperature through the average egg weight $w(x, T^*)$, as
184 well as on the temperature during the first year of the offspring. Putting these com-
185 ponents together, and assuming that half of the fertilized eggs develop to females,
186 the offspring number produced by a female is given by

$$b(x, T, T^*) = 0.5p_m(x)m(x, T^*)s_O(w(x, T^*), T).$$

187 We could not estimate the offspring survival probability $s_O(w, T)$ directly, due
188 to lack of data for the youngest age classes. However, using an estimated time
189 series of the age-specific population densities over the study period (age 3 and
190 older; Langanen et al., 2011), together with the models for growth, survival, and
191 fecundity used in this study, we calculated a rough prediction of the annual off-
192 spring survival probability (Appendix A). From these predicted values the average
193 offspring survival was 0.00028, which is in line with estimates from other studies
194 (on the order of 10^{-4} ; Kipling and Frost, 1970; Wright, 1990; Craig and Kipling,
195 1983). Most of these annual estimates of offspring survival were within the interval
196 0.0001-0.0007 (50 of 53 years; Appendix A). A least squares regression analysis
197 of the annual survival predictions suggested a positive impact of temperature on
198 offspring survival (Appendix A).

199 **SCENARIOS FOR OFFSPRING SURVIVAL**

200 Offspring survival over the first year is influenced by a number of factors (Kamler,
201 1992). In this study we focused especially on temperature and egg weight, and
202 constructed four scenarios for the combined effects of these two variables (Fig. 1).
203 The first year survival also includes the survival of eggs from spawning to hatching.
204 We chose strong effects of egg weight and temperature when included, that would
205 lead to large variation in the survival of offspring in high vs. low temperatures, and
206 from large vs. small eggs (larger than the predicted annual variation in offspring
207 survival, see Appendix A). If the average fitness were found to be insensitive even
208 to such strong effects, this would support the conclusion that their influence is
209 truly weak. However, if the analysis revealed that fitness is potentially sensitive to
210 the temperature effect and/or the egg weight effect on offspring survival, further
211 studies would be needed to evaluate the actual impact of these effects. For all
212 scenarios the mean offspring survival probability was set to 0.00028, as indicated by
213 the predicted values described above. Offspring survival probability was modeled
214 on a logit scale, and parameter values for each scenario are shown in Table 2.

215 For Scenario 1 (“Interaction”) we assumed a negative interaction between egg
216 weight and temperature, where offspring from large eggs have an advantage in
217 colder temperatures but a disadvantage in warmer temperatures. There are a num-
218 ber of potential mechanisms that could lead to such an interaction (Kamler, 1992).
219 For instance, large eggs may be at a disadvantage in lower-oxygen warm conditions
220 due to their lower surface-to-volume ratio. In cold conditions the longer develop-
221 ment times of embryos may give an advantage to large eggs. For the other three
222 scenarios we included a separate effect of egg weight (Scenario 2: “Eggweight”), a

223 separate effect of temperature (Scenario 3: “Temperature”), or no effect of either
224 (Scenario 4: “Constant”). In Scenario 2 offspring from a large egg of 0.006 g would
225 have approximately 24 times higher survival probability than an offspring from a
226 small egg of 0.002 g (see histogram of the observed egg weights in Appendix A),
227 and in Scenario 3 offspring in a warm year of 13°C would have approximately 19
228 times higher survival than those in a cold year of 8°C.

229 **STATISTICAL ESTIMATION OF VITAL RATES**

230 The vital rate functions defining the IPM were estimated from data using mixed
231 effects models (Pinheiro et al., 2013), except for the offspring survival probability
232 (scenarios described above), and the probability of maturity which was assumed
233 to follow a logit function where parameters (Table 2) were chosen to fit the results
234 reported by Frost and Kipling (1967). All analyses were done with the software
235 R (R Development Core Team, 2013). With the exception of egg weight, the vital
236 rates have also been estimated for earlier IPMs for this population (Vindenes et al.,
237 2014; Vindenes and Langangen, 2015). However, as some small modifications were
238 made to the models used in this study, the estimation procedures for all vital rates
239 are described in Appendix B. Here, values of the estimated variance of residuals
240 and year effects are also provided (not used for the IPM analysis), and we discuss
241 some differences between the vital rate models of this study and the results of
242 earlier studies (Edeline et al., 2007; Vindenes et al., 2014).

243 For the vital rate functions estimated by mixed models, several candidate mod-
244 els were fitted for the fixed effects, and model selection was done by comparison
245 of AIC values. Other covariates than the state variables of the IPM were also in-
246 cluded when relevant (capture month, capture year, and somatic condition index),

247 but for the IPM analyses these effects were averaged out (values given in Table
248 3). If competing models had a $\Delta AIC < 2$ the model with fewest parameters was
249 selected. Because maternal identity is unknown in the data, we could not include
250 effects of female offspring length or female current length in the estimation of the
251 offspring length distribution. However, in Appendix C4 we present results for an
252 alternative model assuming a correlation of 0.3 between maternal and offspring
253 length at age 1 (such a correlation could arise due to genetic inheritance and/or
254 maternal effects). The main conclusions from the main model were not altered,
255 but the impacts of some vital rates then increased (in particular, offspring length).

256 For the survival probability model included in the IPM we also added a neg-
257 ative effect of female offspring length (adjusting the intercept to keep the mean
258 constant), which was not estimated directly from the data (a range of values of
259 this effect were explored by Vindenes and Langangen, 2015). Data on capture age
260 suggest that this effect could be negative, which would imply a survival cost of
261 rapid growth since offspring length has a positive effect on somatic growth (Vin-
262 denes and Langangen, 2015). Therefore, we included a negative effect also in the
263 model used here, but note that this assumption is not critical for the results of the
264 elasticity analysis (except for the elasticity to this effect itself, other elasticities
265 remained largely the same if the value of this effect was changed).

266 Because of gillnet sensitivity pike were not captured until they had reached
267 a length of ~ 55 cm. The model for somatic growth was estimated from data on
268 back-calculated lengths and is therefore conditional on survival until capture. Since
269 survival is also length-dependent, the estimated growth rate will be biased upward,
270 especially at small lengths. We estimated the size of the bias and it was not very
271 large (Appendix B). Therefore, we did not correct for it here as it is unlikely to

272 affect the qualitative results or conclusions of this study.

273 SENSITIVITY AND ELASTICITY ANALYSES

274 The sensitivity of λ can be calculated with respect to a point in the projection
275 kernel or with respect to an underlying variable (here: x , y , or T), and shows the
276 expected change in λ due to a small additive perturbation to the focal variable.
277 The corresponding elasticity shows the proportional change in λ to a proportional
278 perturbation (Caswell, 2001). Detailed methods for the sensitivity and elasticity
279 analyses are provided in Appendix C.

280 The sensitivity of λ to a point $K(x'y'; x, y)$ in the projection kernel is given
281 by $v(x', y')u(x, y)$ (Ellner and Rees, 2006), using the above scaling of $v(x, y)$ and
282 $u(x, y)$. The corresponding elasticity is given by $v(x', y')u(x, y)K(x'y'; x, y)/\lambda$. In
283 order to compare the elasticity contributions from each length x , the elasticity
284 kernel was integrated over x' , y' , and y . The sensitivity and elasticity of λ to
285 the three underlying state variables x , y , and T were decomposed into contri-
286 butions from each of the vital rate functions across current length x , using the
287 same approach as that of Vindenes et al. (2014), and the detailed expressions
288 are shown in Appendix C. elasticity results are shown (corresponding sensitivities
289 are shown in Appendix C3). Overall, the elasticity and sensitivity patterns were
290 similar, except when the focal variable was x itself. In that case, the elasticity con-
291 tributions from larger x were relatively higher than the corresponding sensitivity
292 contributions, although the rankings most vital rate contributions remained the
293 same (Appendix C3).

294 The calculations were done numerically by adding a small perturbation (of size
295 $1 \cdot 10^{-5}$) to first evaluate each of the vital rate sensitivities (Appendix C). We

296 checked that this perturbation was small enough that a further reduction did not
297 affect results to the order that they are reported. For each underlying variable
298 we first calculated the sensitivity (and its decomposition), and then found the
299 corresponding elasticity by multiplying the sensitivity with the focal variable and
300 dividing by λ (Appendix C2).

301 The elasticities reported here were calculated for a mean temperature of $T =$
302 10.5°C . In Appendix C3 we also present results for elasticities (and sensitivities)
303 calculated at $T = 9^{\circ}\text{C}$, and at $T = 12^{\circ}\text{C}$, representing a cold and warm year,
304 respectively (see observed temperatures in Appendix A1). Qualitatively most elas-
305 ticity patterns and rankings of vital rate contributions remained the same when
306 calculated at different temperatures, although some differ.

307 **Results**

308 **VITAL RATE FUNCTIONS**

309 Average egg weight increased with female length, but the relationship leveled off
310 and may even decline for the largest lengths (Table 3, Fig. 2A). There was no
311 significant effect of female offspring length on egg weight (Appendix B). Previous
312 temperature had an overall negative effect, which increased with female length.
313 There was also a positive effect of body condition, as expected from earlier studies
314 (Edeline et al., 2007).

315 Fecundity (egg number) was also positively affected by female length, as ex-
316 pected (Table 3, Fig. 2B). There was no significant effect of temperature or female
317 offspring length, but there was a positive effect of body condition. For the egg
318 weight and fecundity functions in the IPM the condition effect was averaged out,

319 together with those of year and capture month (values given in Table 3).

320 Offspring length at age 1 increased with temperature (Table 3, Fig. 2D), as
321 found in earlier studies (Vindenes et al., 2014). Both the growth and the survival
322 models were similar to earlier studies (Vindenes et al., 2014; Vindenes and Lan-
323 gangen, 2015) as only minor adjustments were made here (details in Appendix B).
324 Next year's length was positively influenced by temperature, with stronger tem-
325 perature effects for smaller individuals (Table 3, Fig. 2E). The higher order effects
326 of length were included to correctly capture the growth rate of the largest individ-
327 uals (Appendix B). Offspring length y had a positive effect on growth, as expected
328 (Vindenes and Langangen, 2015), and length differences among offspring tend to
329 persist over age (Appendix B). The estimated growth variance function was given
330 by $\sigma_G^2 = 11.24e^{-0.0081x}$.

331 In line with earlier models, the survival probability was very low for small
332 individuals and then increased rapidly with length until ~ 50 cm (Fig. 2F; Table
333 4; Vindenes et al., 2014). There was an overall negative effect of temperature. A
334 schematic overview of how each underlying state variable (temperature, current
335 length and offspring length) influences each of the vital rates is provided in Fig. 3.
336 For the survival, growth and offspring length functions used in the IPM the year
337 effect was averaged out (values in Table 3).

338 **TOTAL ELASTICITY OF λ ACROSS CURRENT LENGTH**

339 For lengths corresponding to age class 2 and older, the contribution to the elasticity
340 of λ with respect to the projection kernel generally increased with length x . The
341 peaks in the elasticity contribution over x correspond to different age classes, and
342 become less distinctive with length as individuals grow at different rates over their

343 lifetime. Compared to the stable length distribution of x (also shown in Fig. 4), the
344 peaks are shifted towards larger lengths, as within each age class larger individuals
345 contribute more to population growth than smaller ones.

346 The elasticity contribution from offspring (the first peak) is large because they
347 constitute a large proportion of the stable population (Fig. 4). From age 2 and
348 older the elasticity increases with length until around 80 cm, after which it declines
349 towards zero for the largest lengths where the individuals constitute only a small
350 fraction of the stable population (Fig. 4). We can make a rough comparison of the
351 elasticity for mature vs. immature females, by comparing the integrated values for
352 lengths below 42 cm, roughly corresponding to immature females, and above 42 cm
353 corresponding to mature ones. For Scenarios 1, 3, and 4 the elasticity contribution
354 of mature pike was almost four times higher than that of immature pike (~ 0.77 for
355 mature and ~ 0.23 for immature). For Scenario 2 the elasticity contribution from
356 mature females was slightly higher (~ 0.79 for mature and ~ 0.21 for immature).

357 ELASTICITY OF λ TO UNDERLYING VARIABLES

358 The elasticities of λ with respect to the underlying variables of female length x ,
359 female offspring length y , and temperature T ($= T^*$) were decomposed into con-
360 tributions from each vital rate across length x , for each of the four scenarios for
361 offspring survival (Fig. 5). For the elasticity of λ to temperature, the contributions
362 from survival, growth, and offspring length were similar between the four scenarios
363 (Fig. 5A, D, G, J). For growth the largest contributions were from small females,
364 whereas for offspring length the contributions generally increased with the mater-
365 nal length x . For Scenario 1 (Fig. 5A) the largest contribution to this elasticity
366 was from offspring survival, while the smallest was from egg weight. Note that the

367 contribution from offspring survival reflects only the direct temperature effect, as
368 determined by the scenario for offspring survival, and not the indirect effect of tem-
369 perature through egg weight. The latter is shown as a separate contribution. For
370 Scenario 2 the largest contribution was from egg weight (Fig. 5D). For Scenario 3
371 the largest contribution to this elasticity came from offspring survival (Fig. 5G).

372 Considering the elasticity of λ to female length x , the largest contributions
373 were from survival, followed by growth and then fecundity, and these patterns
374 were similar in all four scenarios (Fig. 5B, E, H, K). The survival contributions
375 were larger from small individuals. The growth contributions were large both for
376 small and large pike, while the fecundity contributions increased with length as
377 expected. In all four scenarios the smallest contribution to this elasticity came
378 from the probability of maturity. In Scenario 1 the elasticity contribution from
379 egg weight was only slightly larger (Fig. 5B), while in Scenario 2 assuming a
380 strong effect of egg weight on offspring survival it was somewhat larger (Fig. 5E).
381 However, this contribution was still much lower than those from survival, growth,
382 and fecundity.

383 Finally, considering the elasticity of λ with respect to offspring length y , the
384 contributions from survival and growth looked similar in all four scenarios (Fig. 5C,
385 F, I, L). The survival contribution was negative due to our assumption of a negative
386 effect of offspring length on survival, whereas the growth contribution was positive.
387 The largest contributions to this elasticity were from small lengths.

388 Discussion

389 We have evaluated the relative impacts on the mean fitness (population growth
390 rate) λ from different underlying effects in the life cycle, using an IPM. A main
391 conclusion from the elasticity analysis is that under a wide range of assumptions
392 λ was not sensitive to maternal effects of length on egg weight, even when egg
393 weight had a strong effect on offspring survival (Fig. 5). In contrast, λ was highly
394 sensitive to environmental conditions (here: temperature) experienced in early life.
395 These results do not support the hypothesis that “big old fat fecund female fish”
396 contribute relatively more to population growth than small females (Hixon et al.,
397 2014), however the model included only one of several suggested mechanisms for
398 how maternal size can affect offspring survival. We emphasize that although the
399 maternal size effect on offspring survival had a weak impact on fitness, large females
400 still contribute much to population growth through other vital rates (Fig. 4).

401 There are two main mechanisms underlying the weak impact of the maternal
402 size effect, and both could be general for many size-structured populations. First,
403 in highly fecund size-structured organisms the stable size distribution is typically
404 skewed towards small (young) individuals, so that a large proportion of the off-
405 spring will be produced by small (young) mothers, at least on average. Offspring
406 produced by the few large females must have a much higher survival than those
407 from small females if the survival difference is to have any sizeable impact on the
408 population growth (Hixon et al., 2014). If such large survival differences occurred
409 consistently, it would also induce a selection pressure for small females to delay
410 reproduction. The fact that small females still invest energy in reproduction sug-
411 gests that the survival difference of offspring due to maternal size is usually not

412 very large. Second, the maternal length effect on egg weight was rather weak and
413 leveled off with length (Fig. 2C). However, this pattern may also be general for
414 fish, as many studies on different species have revealed a similar shape where the
415 egg size levels off or even declines for the largest (oldest) females (Kamler, 2005).
416 In Appendix C5 we explored how the sensitivity results would change for a model
417 assuming a stronger, linear effect of maternal length on egg weight. The elasticity
418 contribution from this maternal effect was then larger in particular for Scenario 2,
419 but still moderate compared to the contributions from survival and growth. Thus,
420 given both a strong linear effect of female length on egg weight and a strong ef-
421 fect of egg weight on offspring survival, both of which seem rather unrealistic, the
422 elasticity contribution from this maternal effect can become more substantial.

423 While the offspring produced have mothers of different size, they all experience
424 similar environmental conditions (assuming no spatial environmental heterogene-
425 ity), which contributes to explain why λ was found to be more sensitive to impacts
426 of temperature effects than maternal size effects in early life. Comparing elasticities
427 to length and temperature should be done with caution, however, since these vari-
428 ables have different scales and distributions. The comparison implicitly assumes
429 that the same proportional perturbation is equally likely to occur for the variables
430 of temperature and length. If a perturbation is less likely for temperature than
431 for length, for instance, the relative impacts of temperature compared to length
432 will also be lower than suggested by our results. Note that comparisons of vital
433 rate contributions within each elasticity (i.e. to temperature, current length, and
434 offspring length) can still be done without this limitation.

435 In an unpredictable environment where years that are favorable to offspring
436 survival and growth may occur only rarely, having multiple reproductive events

437 during the lifetime can be a good life history strategy (Roff, 1992; Stearns, 2000).
438 In such life histories individuals invest more energy to their own survival (i.e.
439 maintenance) and growth, which is also reflected in these results as the elasticity
440 contributions were generally larger from survival and growth compared to those of
441 vital rates affecting offspring number (Fig. 5). Among the vital rates determining
442 offspring number, the largest elasticity contributions were from fecundity, which
443 is in line with the assumption that females in highly fecund fish sacrifice offspring
444 survival for increased numbers (Smith and Fretwell, 1974; Einum and Fleming,
445 2000). The hypothesis that large and old female fish contribute more to population
446 growth relative to their biomass has generally been applied to long-lived species,
447 since a longer life span means a greater potential for size (and certainly age)
448 differences to occur (Green, 2008; Hixon et al., 2014). However, mean fitness is
449 expected to be relatively more sensitive to vital rates affecting offspring number
450 in short-lived than in long-lived species (Roff, 1992). Thus, maternal effects of size
451 could potentially be more important to population growth in short-lived species, if
452 maternal size differences are present and have a large effect on offspring survival.

453 Based on a detailed generic model for pike developed to explore consequences
454 of different size-based management scenarios, Arlinghaus et al. (2010) also found
455 only a moderate difference in the results when a maternal size effect on offspring
456 survival was included. In another recent study on pike, Pagel et al. (2015) reported
457 maternal effects on offspring length linked to the mother's growth rate as young
458 but did not find any impacts of her current length. In Appendix C4 we consid-
459 ered effects of a positive correlation between maternal and offspring length (due
460 to genetic inheritance or maternal effects) in our model, partly reflecting this situ-
461 ation. The main conclusion remained the same, as the elasticity contribution from

462 the maternal length effect on egg weight was still small. Maternal effects that are
463 not limited to age or size, but instead reflect some other property of the mother,
464 could potentially be more important to population growth, since the proportion
465 of mothers with the trait in question may not be as restricted.

466 This study has focused on average fitness, measured as the long-term popula-
467 tion growth rate in a density independent structured model. Such models capture
468 average life history properties well (Caswell, 2001), but evaluating more short-term
469 consequences would require extension of the model to explicitly include density
470 dependence as well as stochastic fluctuations in vital rates (Sæther and Engen,
471 2015). Density dependence can be important in early life stages, in particular for
472 pike where cannibalism occurs from a small size (Giles et al., 1986). A regression
473 analysis on our predicted annual offspring survival probabilities suggested a neg-
474 ative effect of intracohort density, in addition to a positive effect of temperature
475 (Appendix A). Effects of density could potentially also interact with the effects
476 of temperature or maternal size. For instance, Kotakorpi et al. (2013) reported
477 that maternal length effects on egg weight were stronger in exploited (low-density)
478 populations, suggesting that large females may be better able to exploit conditions
479 of high per capita resource levels. Using the annual density estimates of Langan-
480 gen et al. (2011) for Windermere pike, where exploitation levels are low, we found
481 no significant effects of density on egg weight or fecundity (not shown), suggest-
482 ing that intracohort density may be more important than intercohort density (i.e.
483 effects of parental density on offspring vital rates). It is also possible that the fe-
484 male size effects on offspring survival are more important to short-term population
485 growth. If transient fluctuations in the size structure are large, the proportion of
486 large females can become high in some years, which could increase the total impact

487 of maternal size effects for population growth. Fishery management often focuses
488 on identifying strong year classes (cohorts) that may dominate the population for a
489 long time and create such transient fluctuations. However, previous research from
490 Windermere suggests that variation in year class strength is not very strong for
491 pike, potentially because of cannibalism (Kipling and Frost, 1970; Kipling, 1976;
492 Paxton et al., 2009; Craig, 1996, 2008).

493 Disentangling the underlying components to fitness can be challenging, in par-
494 ticular when individual life history differences are partly generated by early life
495 conditions. The many studies from different taxa reporting such early life effects
496 on the life history suggest that they are ubiquitous in natural populations (Roff,
497 1996; Lindström, 1999; Lummaa and Clutton-Brock, 2002; Metcalfe and Mon-
498 aghan, 2001; Beckerman et al., 2002). Including the knowledge of early life effects
499 in population dynamical models can therefore be essential to increase our under-
500 standing of the ecology and life history evolution of many organisms. Demographic
501 models such as IPMs are ideal frameworks for incorporating early life effects in
502 structured population models (Plard et al., 2015; Vindenes and Langangen, 2015),
503 and long-term individual based data are essential to these approaches (Clutton-
504 Brock and Sheldon, 2010). While we emphasize that fitness may be sensitive to
505 other vital rates of large females (Figs. 4, 5), our main conclusion from the cur-
506 rent analysis is that maternal size effects on offspring survival likely have a much
507 smaller impact on fitness than environmental conditions during early life. These
508 results are relevant for the population ecology and management of other long-lived
509 top-predators, such as many commercially important fish species.

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518 Data accessibility

519 The data sets used in this study are published online by the Centre for Ecol-
520 ogy & Hydrology (NERC Environmental Information Data Centre; Winfield and
521 Fletcher, 2013; Winfield et al., 2013a,b, 2015).

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675 **Supporting information**

676 The following Supporting Information is available for this article online: Appendix A-
677 C.

678 **Figure captions**

679 **Figure 1**

680 Annual offspring survival probability $S_O(w, T)$ (from egg to age 1) under four
681 scenarios for the effects of current temperature T and egg weight w . Dashed grey
682 lines indicate the average offspring survival probability (0.00028 for all scenarios).
683 A. Scenario 1 (“Interaction”), with a negative interaction between temperature
684 and egg weight, where offspring from large eggs have an advantage under cold
685 conditions but a disadvantage in warm conditions. B. Scenario 2 (“Eggweight”),
686 with a positive effect of egg weight (note different y -axis scale) but no temperature
687 effect. C. Scenario 3 (“Temperature”), with a positive effect of temperature but no
688 effect of egg weight. D. Scenario 4 (“Constant”), with no effect of either temperature
689 or egg weight.

690 **Figure 2**

691 Vital rates as functions of current female length x , shown for three different tem-
692 peratures where relevant (T^* represents temperature in the previous year, and T
693 temperature in the current year). A. Egg weight $w(x, T^*)$ (g). B. Fecundity $m(x)$
694 (egg number). C. Probability of maturity $p_m(x)$. D. Offspring length distribution
695 (length at age 1) $f(x', T)$. E. Mean of next year’s length $\mu_G(x, y, T)$ (assuming
696 $y = 23$ cm). F. Survival probability $s(x, y, T)$ (assuming $y = 23$ cm).

697 **Figure 3**

698 A schematic overview of how each of the state variables in the IPM (female off-
699 spring length y , female current length x , current temperature T , and previous

700 temperature T^*) affects each of the vital rate functions, resulting in the four main
701 vital rates defining the projection kernel. The effect of temperature and egg weight
702 on offspring survival is unknown, and four scenarios are considered in the analyses.
703 The $+/-$ signs indicate whether each effect is predominantly positive or negative,
704 but note that some effects are non-linear or interact with other effects (e.g., the
705 temperature effect on survival depends on female current length). Dotted grey lines
706 represent offspring survival scenarios, where the effects were not estimated from
707 data (see main text and Fig. 1).

708 **Figure 4**

709 Total elasticity of λ to population growth contributions of individuals of length x ,
710 for the four scenarios representing different assumptions on how offspring survival
711 depends on temperature and egg weight (Fig. 1). Note that results corresponding
712 to scenarios 3 and 4 are not distinguishable. The green line is the stable length
713 distribution (y -axis shown to the right), which looks similar for all scenarios.

714 **Figure 5**

715 Elasticity of λ with respect to underlying variables of temperature T ($= T^*$, A,
716 D, G, J), female length x (B, E, H, K), and female offspring length y (C, F, I,
717 L), decomposed into contributions of different vital rates across female length x .
718 The total contribution from each vital rate (integrated over x) is shown in the
719 legends, ranked according to the absolute value. Each row represents one of the
720 four scenarios for offspring survival (A-C: Scenario 1; D-F: Scenario 2; G-I: Scenario
721 3; J-L: Scenario 4). The contribution from offspring survival to the temperature
722 elasticity (panels A and G) reflects only the effect of temperature experienced in

723 the first year, as determined by the scenario, and not the temperature effect on
724 egg weight (the contribution through egg weight is shown separately if non-zero;
725 panels A, D).

726 Tables

Table 1: Overview of state variables and vital rates in the IPM, and model outputs calculated from the projection kernel (assuming constant temperature $T = T^*$).

| | |
|---|--|
| State variables | |
| x | Current female length (cm). |
| x' | Next year's length. |
| y | Female offspring length (length at age 1). |
| y' | Next year's offspring length ($y' = y$ for all except offspring). |
| T | Current temperature ($^{\circ}\text{C}$). |
| T^* | Previous temperature ($T^* = T$ for constant temperature). |
| Vital rates | |
| $s(x, y, T)$ | Annual survival probability. |
| $b(x, T, T^*)$ | Offspring number (#1-year old female offspring per female), |
| - $m(x, T^*)$ | -Fecundity (egg number), |
| - $w(x, T^*)$ | -Average egg weight (g), |
| - $s_O(w(x, T^*), T)$ | -Annual offspring survival probability (from egg to age 1), |
| - $p_m(x)$ | -Probability of maturity. |
| $g(x'; x, y, T)$ | Distribution of next year's length x' (truncated lognormal), |
| - $\mu_G(x, y, T)$ | -Mean of x' , |
| - $\sigma_G^2(x)$ | -Variance of x' . |
| $f(y'; T)$ | Distribution of offspring length at age 1, |
| - $\mu_1(T)$ | -Mean of y' , |
| - σ_1^2 | -Variance of y' . |
| Projection kernel and outputs (evaluated for constant temperature) | |
| $K(x', y'; x, y)$ | Projection kernel. |
| λ | Mean population growth rate/ average fitness for a given constant temperature. |
| $u(x, y)$ | Joint stable distribution of x and y . |
| $v(x, y)$ | Reproductive value as a function of x and y . |
| $K(x', y'; x, y)u(x, y)v(x', y')/\lambda$ | Elasticity of λ to projection kernel. |

Table 2: Underlying effects of temperature and egg weight on offspring survival in the four scenarios (Fig. 1), and underlying effect of current length on probability of maturity (Fig. 2C), both components in offspring number at age 1.

| Vital rate | Scenario | Effect | Value |
|--------------------------------|-------------------------------|---------------------------------|--------------|
| logit(Offspring survival) | Scenario 1 ("Interaction") | Intercept | -7.823 |
| | | Temperature | 0.7 |
| | | Egg weight | 1500 |
| | | Egg weight \times Temperature | -130 |
| | Scenario 2 ("Eggweight") | Intercept | -2.820 |
| | | Egg weight | 800 |
| | Scenario 3 ("Temperature") | Intercept | -6.300 |
| | | Temperature | 0.5 |
| | Scenario 4 ("Constant") | Intercept | 2.2e-4 |
| | | | |
| logit(Probability of maturity) | - | Intercept | -20 |
| | | Length | 0.4 |

Table 3: Fixed effects and statistical significance (marginal tests) for the vital rate models estimated by mixed models (model selection was done based on AIC comparison, see Appendix B). Covariates considered were current female length x , female offspring length y , current temperature T , previous temperature T^* , capture month Mo , capture year Yr , and somatic condition index C . The latter three were fixed at their mean values in the IPM analyses (for fecundity and egg weight: $C = 100$, $Mo = 11.4$, $Yr = 1982$, for offspring length $Yr = 1965$, for growth $Yr = 1966$).

| Vital rate | Fixed effect | Estimate (SE) | F-value (df den) | p-value |
|-------------------------------------|--------------|--|------------------|---------|
| Egg weight $w(x, T^*)$ | (Int) | 6.07 (1.78) | 11.65 (3648) | 0.0006 |
| | x | $-1.20 \cdot 10^{-3}$ ($2.77 \cdot 10^{-4}$) | 18.63 (3649) | <.0001 |
| | x^2 | $-6.15 \cdot 10^{-7}$ ($7.74 \cdot 10^{-8}$) | 63.21 (3649) | <0.0001 |
| | Mo | $4.51 \cdot 10^{-4}$ ($2.50 \cdot 10^{-5}$) | 324.84 (3649) | <0.0001 |
| | C | $9.56 \cdot 10^{-6}$ ($8.88 \cdot 10^{-7}$) | 115.92 (3649) | <0.0001 |
| | T^* | $5.24 \cdot 10^{-4}$ ($1.32 \cdot 10^{-4}$) | 15.75 (37) | 0.0003 |
| | Yr | $-6.08 \cdot 10^{-3}$ ($1.79 \cdot 10^{-3}$) | 11.47 (37) | 0.0017 |
| | Yr^2 | $1.52 \cdot 10^{-6}$ ($4.53 \cdot 10^{-7}$) | 11.23 (37) | 0.0019 |
| | $x : Yr$ | $7.21 \cdot 10^{-7}$ ($1.49 \cdot 10^{-7}$) | 23.42 (3649) | <0.0001 |
| | $x : T^*$ | $-1.12 \cdot 10^{-5}$ ($2.35 \cdot 10^{-6}$) | 22.50 (3649) | <0.0001 |
| Fecundity $\sqrt{m(x)}$ | (Int) | $-3.63 \cdot 10^5$ ($5.06 \cdot 10^4$) | 51.42 (3651) | <0.0001 |
| | x | $-8.15 \cdot 10$ ($1.07 \cdot 10$) | 58.23 (3651) | <0.0001 |
| | Mo | 1.63 ($4.98 \cdot 10^{-1}$) | 10.74 (3651) | 0.0011 |
| | C | $7.90 \cdot 10^{-1}$ ($4.65 \cdot 10^{-2}$) | 284.25 (3651) | <0.0001 |
| | Yr | $3.69 \cdot 10^2$ ($5.11 \cdot 10$) | 52.2 (38) | <0.0001 |
| | Yr^2 | $-9.40 \cdot 10^{-2}$ ($1.29 \cdot 10^{-2}$) | 53.12 (38) | <0.0001 |
| | xYr | $5.43 \cdot 10^{-2}$ ($5.39 \cdot 10^{-3}$) | 70.77 (3651) | <0.0001 |
| Mean offspring length $\mu_1(T)$ | (Int) | $-6.34 \cdot 10$ ($2.21 \cdot 10$) | 8.21 (7857) | 0.0550 |
| | T | $6.53 \cdot 10^{-1}$ ($2.74 \cdot 10^{-1}$) | 5.67 (47) | 0.0213 |
| | Yr | $4.06 \cdot 10^{-2}$ ($1.16 \cdot 10^{-2}$) | 12.28 (47) | 0.0010 |
| Growth mean $\mu_G(x, y, T)$ | (Int) | $-1.01 \cdot 10^2$ ($2.00 \cdot 10$) | 70 (25877) | <0.0001 |
| | x | 2.79 ($4.36 \cdot 10^{-2}$) | 4086 (25877) | <0.0001 |
| | x^2 | $-4.54 \cdot 10^{-2}$ ($1.24 \cdot 10^{-3}$) | 1335 (25877) | <0.0001 |
| | x^3 | $4.59 \cdot 10^{-4}$ ($1.51 \cdot 10^{-5}$) | 919 (25877) | <0.0001 |
| | x^4 | $-1.59 \cdot 10^{-6}$ ($6.49 \cdot 10^{-8}$) | 598 (25877) | <0.0001 |
| | y | $3.71 \cdot 10^{-1}$ ($1.21 \cdot 10^{-2}$) | 939 (25877) | <0.0001 |
| | Yr | $4.078 \cdot 10^{-2}$ ($6.25 \cdot 10^{-3}$) | 43 (45) | <0.0001 |
| | T | 1.32 ($1.58 \cdot 10^{-1}$) | 70 (45) | <0.0001 |
| | $x : T$ | $-1.42 \cdot 10^{-2}$ ($1.26 \cdot 10^{-3}$) | 126 (25877) | <0.0001 |
| | $x : y$ | $-4.10 \cdot 10^{-3}$ ($2.21 \cdot 10^{-4}$) | 344 (25877) | <0.0001 |

Table 4: Fixed effects for the survival probability model, estimated on a logit scale. The covariates are current female length x , female offspring length y , temperature T , and capture year Yr ($Yr = 1972$ in the IPM). The mean and standard deviations are based on 1000 realizations of a Monte Carlo resampling procedure (histogram and correlation plots for effects are shown in Appendix B).

| Effect | Estimate (SE) |
|---------------|--|
| (Int) | $7.33 \cdot 10^{-1}$ (3.58) |
| x | $4.89 \cdot 10^{-1}$ ($3.89 \cdot 10^{-2}$) |
| x^2 | $-3.74 \cdot 10^{-3}$ ($1.27 \cdot 10^{-4}$) |
| T | $1.93 \cdot 10^{-1}$ ($1.84 \cdot 10^{-1}$) |
| Yr | $-4.37 \cdot 10^{-2}$ ($1.31 \cdot 10^{-3}$) |
| $x : T$ | $-6.84 \cdot 10^{-3}$ ($3.48 \cdot 10^{-3}$) |
| y | $-5 \cdot 10^{-2}$ |









