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

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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

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the mean fitness (population growth rate  $\lambda$ ) 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  $\lambda$  to the projection kernel, and ii) the elasticity of  $\lambda$  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,  $\lambda$  was largely insensitive to this effect, even when egg weight was assumed to have a strong effect on offspring survival. In contrast,  $\lambda$  was sensitive to early temperature conditions through growth and survival. Among mature females, the total elasticity of  $\lambda$  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 (Metcalf 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  $\sim 41.5$  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  $\lambda$  (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  $\sim 55$  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  $\lambda$  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  $\lambda$  due to a small additive perturbation to the focal variable.  
277 The corresponding elasticity shows the proportional change in  $\lambda$  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  $\lambda$  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  $\lambda$  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  $\lambda$  (Appendix C2).

301 The elasticities reported here were calculated for a mean temperature of  $T =$   
302  $10.5^{\circ}\text{C}$ . 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  $\sim 50$  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 $\lambda$ ACROSS CURRENT LENGTH**

339 For lengths corresponding to age class 2 and older, the contribution to the elasticity  
340 of  $\lambda$  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 ( $\sim 0.77$  for  
355 mature and  $\sim 0.23$  for immature). For Scenario 2 the elasticity contribution from  
356 mature females was slightly higher ( $\sim 0.79$  for mature and  $\sim 0.21$  for immature).

### 357 ELASTICITY OF $\lambda$ TO UNDERLYING VARIABLES

358 The elasticities of  $\lambda$  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  $\lambda$  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  $\lambda$  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  $\lambda$  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)  $\lambda$  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  $\lambda$  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,  $\lambda$  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  $\lambda$  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  $\lambda$  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  $\lambda$  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  $T = T^*$ ).

<b>State variables</b>	
$x$	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).
<b>Vital rates</b>	
$s(x, y, T)$	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 $y'$ ,
- $\sigma_1^2$	-Variance of $y'$ .
<b>Projection kernel and outputs (evaluated for constant temperature)</b>	
$K(x', y'; x, y)$	Projection kernel.
$\lambda$	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 $\lambda$ 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.

<b>Vital rate</b>	<b>Scenario</b>	<b>Effect</b>	<b>Value</b>
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).

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











