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Skilbrei, O.T. and Heino, M.

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Ove T. Skilbrei (ove.skilbrei@imr.no)
Mikko Heino (mikko.heino@imr.no)

Approved by

Ulf Dieckmann
Program Leader, EEP

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4 Ove T. Skilbrei[a]* and Mikko Heino[abc]

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6 [a]Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway.

7 [b]Department of Biology, University of Bergen, Box 7803, N-5020 Bergen, Norway

8 [c]Evolution and Ecology Program, International Institute for Applied Systems Analysis

9 (IIASA), A-2361 Laxenburg, Austria

10

11 *Corresponding author, Tel.: +47 55236894; fax: +47 55 23 85 31 Email address:

12 ove.skilbrei@imr.no

13

14 **Abstract**

15 To study relationships between fish length, photoperiod and the onset of precocious maturity

16 in 0+ parr during intensive rearing of Atlantic salmon (*Salmo salar* L.), 0+ juveniles of 62–82

17 mm length were individually tagged with Passive Induced Transponders (PITs) in May and

18 exposed to reduced daylength (LD12:12) in May, June or July, or kept as control fish under

19 continuous light. Relationships between the length of the fish and maturity were studied by

20 the use of probabilistic maturation reaction norms. The incidence of mature males and the

21 proportion of fish of lower modal group size in autumn were highest in the groups exposed to

22 short days in May, and lowest under continuous light. In contrast with the expectation that

23 high growth rates promote maturation, the future mature male parr were smaller than the

24 immature males at the start of the experiment, and they also grew more slowly during the

25 subsequent maturation process. Variability in condition factor was low until autumn, when

26 the condition factor of maturing males rose well above that of immature males during autumn

27 as the fish grew from ~ 80 to ~ 95 mm length. Reduced daylength increased the probability of

28 the onset of precocious maturity in the fish smaller than, but not above a threshold length of

29 ~ 90–100 mm (9–11 g). Intensively reared parr of 60–90 mm, and possibly also smaller fish,

30 may be particularly sensitive to photoperiod manipulations that may influence the

31 probabilities of fish adopting one of the three life-history alternatives, to enter lower or upper

32 mode or to mature precociously.

33

34 Key words: Mature male parr, threshold length, probabilistic maturation reaction norms, fish

35 culture, growth, bimodality

36

37 **1. Introduction**

38

39 The high degree of adaptive flexibility displayed by Atlantic salmon (*Salmo salar* L.) is

40 exemplified by the existence of a life-history strategy that includes a reproductive cycle in

41 male parr while they still live in freshwater. It is generally accepted for many fish species that

42 growth rate is positively correlated with an increased probability of maturation (Alm, 1959;

43 Taranger et al., 2010), and improved conditions for growth increase the proportion of mature

44 male parr in hatcheries (Leyzerovich, 1973). Experiments with 1+ juvenile salmon have

45 confirmed that rapid growth may result in early maturation in male parr (e.g. Rowe and

46 Thorpe 1990; Berglund 1992). Condition factor in spring has also been positively related to

47 the incidence of maturation in 1+ parr (Saunders and Duston 1997), but not in 0+ parr

48 (Duston et al. 2005).

49 Precocious maturation represents a production loss in commercial hatchery production due to

50 reduced growth and negative interference with smoltification (Thorpe and Morgan, 1980;

51 Duston and Saunders, 1992; Saunders et al., 1994). The introduction of more intensive

52 rearing methods implementing increased temperature and photoperiod manipulations to

53 produce underyearling smolts has also accelerated the developmental rates of parr that mature

54 precociously. Rearing protocols normally involve the fish being first fed under continuous

55 light, after which the photoperiod is reduced during the summer before being raised again in

56 autumn to synchronize the smoltification process (Saunders et al. 1990; Berge et al. 1995;

57 Duston and Saunders 1995). The use of short daylengths during the first summer has been

58 shown to stimulate precocious maturation to various degrees, depending on the timing and

59 duration of the short day treatment (Duston and Saunders, 1992; King et al., 2003; Berrill et

60 al., 2003; 2006; Nordgarden et al., 2007).

61 The relationships between growth rate, fish size and probability of precocious

62 maturation are complex, because of the dynamic growth pattern that salmon in culture

63 display. This often produces a bimodal length-frequency distribution during their first year of

64 life, with an upper mode of smolts and a lower mode of more slowly developing parr

65 (Thorpe, 1977; Kristinsson et al., 1985; Skilbrei, 1988). It is not clear to what extent the onset

66 of precocious maturation is directly related to size, or to the two alternative developmental

67 routes of the lower and upper mode fish. Studies of threshold sizes for parr maturation have

68 usually described size variation among wild sexually mature parr (Aubin-Horth and Dodson,

69 2004; Baum et al., 2004, 2005). However, the correlation between the size of the male at the

70 onset of maturity, and its size when it is sexually mature, probably varies greatly with the

71 opportunities for growth experienced by the fish during the maturation process.

72 There is a lack of more detailed information on relationships between fish size,

73 reduction in photoperiod and onset of precocious maturity under intensive rearing conditions.

74 The purpose of the present study was to provide this kind of information, by studying the

75 response of individually tagged cultured parr that were exposed to a shortened photoperiod at

76 various dates during their first spring and summer under favourable conditions for growth.

77

78 **2. Materials and Methods**

79

80 *2.1. Fish and experimental treatments*

81

82 Three family groups that were offspring of 2-sea-winter salmon of the domesticated Aqua

83 Gen strain were used. Eyed eggs were incubated in darkness. The fish were first fed on 5

84 March and kept under continuous light until the start of the experiment at Matre Research

85 Station. A total of 1500 individuals with a mean length of 74±5 mm, 500 from each family,

86 were tagged with Passive Induced Transponders (PIT) (size: 2x12 mm, Trovan®) in late

87 May. The fish were anaesthetized with benzocain. A small cut was made with a scalpel to

88 insert the tag into the body cavity. The wound was treated with the antibiotic nitrofurazone to

89 prevent bacterial infections. The fish were distributed equally into eight 1x1 m 300 l square

90 tanks (187–188 individuals per tank). These tanks were the experimental units, whereas the

91 observational unit was a single fish.

92   To check whether the PIT tags affected the development of the fish, a further 70 fish

93 from each of the three families were fin-clipped differently (unclipped and left and right

94 pelvic fin) and supplied to each tank. To reduce the density of fish in the tanks, the numbers

95 were reduced to ~ 50 fish per family per tank on 29 September. Due to mortality in one tank

96 after one week (25 % of fish), and rejections of individual data points due to error readings

97 (of tag code, length or weight), 1360 individually tagged fish and 1013 fin-clipped fish were

98 finally used for analysis.

99   The fish were tagged on 21–23 May. Length and size were also measured on 23–25

100   June, 15–22 July, 30 Sept–2 Oct, on 24–26 November and finally on 19 January when all the

101   fish were killed and gonads examined. The fish were held under continuous light from first

102   feeding until the start of the experiment. Photoperiod was reduced to 12 hours of daily light

103   in parallel tanks on three successive dates during summer; on 23 May, on 25 June and on 22

104   July, while controls were kept under continuous light (PR-May, PR-June, PR-July and P24).

105   The fish were held under these four photoperiods until the end of the experiment. The fish

106   were fed commercial dry pellets by automatic feeders 12 h per day from the start of the

107   experiment in late May.

108   Mean temperature and monthly means were 13.2 °C from first feeding to the start of

109   the experiment. From June to October, the mean temperature was 12.7 °C, with a variation

110   from 11.5 to 14.1 °C between months. It then declined during autumn to 8.4 °C in November,

111   6.7 °C in December and 5.8 °C in January.

112

113   *2.2. Data treatment and statistical analyses*

114

115   On the basis of inspection of the length-frequency distributions the lower mode fish were

116   defined as those smaller than 145 mm in November (Fig. 1).

117   The GLM (General Linear Models) module of the statistical package STATISTICA

118   (Statsoft 2008) was applied for one-way and multiple analysis of variance in length, condition

119   factor and specific growth rate in different treatment groups and parallel tanks (as random

120   effect), and for multiple *post hoc* comparisons to test means of specific groups (Newman-

121   Keuls). The lme4 package by Bates and Mechler (2010) under R 2.11 was used to fit

122   Generalized Linear Mixed Models (GLMM) with a logistic link function to test for

123   differences in the incidence of mature male parr and for variability in the proportion of lower

124   modal group fish.

125   In estimating the effects of marking on maturation and probability of being a lower

126   modal group fish, marking method and experimental treatment were treated as fixed effects

127   and family and tank were treated as random effects. In estimating size-dependent maturation

128   probabilities (i.e., probabilistic maturation reaction norms, see Heino et al., 2002), size was a

129   variate, experimental treatment was a fixed effect, and family and tank were random effects.

130   However, because the tank effect was never significant, this effect was not included in any of

131   the final models. Size was measured as both length and weight. Both measures are good

132   predictors of maturation, and our results are qualitatively independent from the choice of size

133   metric. For simplicity, we focus here on length − models using length were slightly better

134   than those using weight (ΔAIC~1 in favour of length). Appendix A gives the main results for

135   both length- and weight-based estimations.

136

137   Specific growth rate (SGR) and condition factor (C) were calculated according to the

138   formulas:

139   SGR (% d^{-1})=100×(ln(W_2)−ln(W_1))/(t_2−t_1),

140   where W_2 and W_1 are the weights (g) of the individual at day t_2 and t_1, respectively.

141   C1=100×W_1/L_1^3

142   where L_1 is fork length in cm.

143

144   **3. Results**

145

146   *3.1 Proportions of mature male parr and lower modal group fish*

147

148   The proportions of mature male parr were highest following the reduction in photoperiod in

149   May, and were halved during the subsequent two reductions (Table 1). The control group

150   performed comparably to the PR-July group. The proportion of lower modal group fish

151   declined in a similar way, except that the PR-June and PR-July treatments were almost

152   identical and that P24 contained only one fifteenth of the lower mode fish in PR- May (Table

153   1). Family A produced the highest proportions of both mature male parr (Table 1) and lower

154   modal group fish among immature fish (15.7% vs 2.5 and 2.0% in Families B and C,

155   respectively). Treatment and family significantly affected both the incidences of mature male

156   parr and the percentages of lower mode fish (both GLMM binomial response models:

157    $p_{treatment}$, $p_{family} < 0.0001$). There were no significant contributions from rearing the fish in

158   parallel tanks in either model ($p_{tank} = 0.70$ and 0.56, respectively). The differences between

159   the groups tagged with PITs or fin-clips were insignificant for the incidence of mature males

160   ($p_{Mark} = 0.96$), and close to significance for the lower mode fish ($p_{Mark} = 0.053$). The use of

161   PIT tags therefore appeared to be of minor importance for the development of the fish.

162

163   *3.2 Length-dependent response to photoperiod*

164

165   The immature future lower modal group fish of the PR-May treatment had a mean length of

166   69 ± 4 mm in late May, as opposed to 75 ± 5 mm of the fish that entered the upper mode (t-

167   test, $p < 0.0001$).

168   Maturity in the end of the experiment was significantly explained by length in May

169   (likelihood ratio test: d.f.=1, p<0.0001), with the probability of maturing being a decreasing

170   function of length (Fig. 2). Reduced daylength resulted in increased tendency to mature

171   (likelihood ratio test: d.f.=3, p=0.006). This effect became weaker the later light regime was

172   manipulated, and the effect was not significant for fish exposed to reduced daylength in July.

173   At the same time, there were large differences between the families (Fig. 2).

174   Fish that were exposed to reduced daylength in May showed increased maturation

175   tendency relative to the control fish (d.f.=1, p=0.0017), but this increase was length-

176   independent: the interaction between treatment and length was insignificant (d.f.=1, p=0.32)

177   and the odds on maturing in the final model thus length-independent (Fig. 3). However, the

178   fish that were exposed to reduced daylength in June showed a length-dependent response: the

179   model with length-treatment interaction was significantly better than one without (d.f.=1,

180   p=0.027). Fish that were less than about 90 mm in length in June responded to reduced

181   daylength by increasing their maturation tendency, whereas larger fish had an opposite

182   response (Fig. 3). Similar results were obtained for daylength change in July (p=0.012 for the

183   length-treatment interaction), although the threshold below which maturation was facilitated

184   was shifted upwards to around 100 mm. In summary, reduced daylength facilitates

185   maturation, but only so below a threshold of about 90–100 mm. The corresponding thresholds

186   in weight were 7-11 g (see Appendix A; Table A1 and Figs A1 and A2).

187

3.3 Influence of photoperiod and maturity on growth and condition

189

190 Only the maturing and immature males of family A and B were used for further treatment of

191 the data in figures 4 and 5 and statistics shown in Table 2 due to the low incidence of mature

192 male parr in family C. With one exception, the use of parallel tanks did not contribute

193 significantly to any of the multiple analyses of variance in length, condition factor and

194 growth rate, and was not included in the reported models (Table 2). The exception was

195 caused by significant differences in growth rates of the fish in parallel tanks under the PR-

196 June treatment during the two last measurements (p<0.05, Newman-Keuls multiple test).

197

198

3.3.1 Size and growth rates of males

200

201 The future mature males of family A and B were significantly smaller than the immature

202 males at the start of the experiment in May, 69±4 mm (mean±SD) versus 74±5 (p<0.05,

203 Newman-Keuls tests). These differences in initial length contributed significantly to the

204 multiple analyses of variance, and increased during the experiment because of the clearly

205 higher growth rates of immature fish (Table 2, Fig. 4).

206 The growth rates of the future mature males dropped shortly after reductions in

207 photoperiod (Fig. 4). The growth rates of PR-May, PR-June and PR-July were significantly

208 lower than the P24 maturing males starting from the first, second and third period of

209 measurement, respectively (p<0.05, Newman-Keuls tests), and as a result, the P24 mature

210 males were significantly larger than the other mature males at the end of the experiment

211 (p<0.05, Newman-Keuls tests). Due to these developmental characteristics, maturity

212 significantly affected the variability in length and growth rates at all periods. The effect of

213 photoperiod was weaker (lower F values), and did not significantly affect length before the

214 third measurement in July (Table 2). Interactions between maturity and photoperiod were

215 weak in most cases and did not seem to be important for the overall results (Table 2).

216

217 *3.3.2 Development in condition factor of males*

218

219 There was no significant variation in condition factor at the start of the experiment between

220 the immature males and the future mature males. Significant effects of either maturity or

221 photoperiod were seen in June and July, but the contributions from both factors to total

222 variability became much clearer during the autumn, when the condition factor of maturing

223 males rose well above that of immature males as the fish grew from ~ 80 to ~ 95 mm length

224 (Table 2, Fig.5). A significant interaction between maturity and photoperiod also developed

225 during the autumn (Table 2), partly because of a negative relationship between the condition

226 factor of maturing males and the duration of the period they had been held under 12 hours of

227 daily light (Condition factor of PR-May < PR-June < PR-July and P24; $p<0.05$, Newman-

228 Keuls tests).

229

230 *3.3.3 Growth rates of males in comparison to females*

231

232 Possibly because of higher probability of maturation in the PR-May treatment group among

233 initially smaller, slow-growing males (see above), the remaining immature males comprised

234 more rapidly growing fish. They grew faster than the females during the first three periods

235 from May to October (mean specific growth rates of immature males and females were

236   1.59 ± 32 d^{-1} and 1.44 ± 0.39 d^{-1} from May to October) and were larger than the females from

237   on June (immature males and females weighted 9.3 ± 0.3 g and 8.5 ± 0.3 g in June, and

238   39.4 ± 1.4 g and 35.3 ± 1.8 g in early October) (Newman-Keuls tests, $p < 0.05$). Immature males

239   and females of the other treatment groups were not significantly different.

240

241   **4. Discussion**

242

243   Reductions in daylength triggered precocious maturation in male parr reared under intensive

244   hatchery conditions, and the growth rates of the maturing males declined shortly after the

245   photoperiod adjustments. This study is the first to demonstrate a clear relationship between

246   the probability of onset of maturity in 0+ male parr and its length when photoperiod was

247   reduced.

248   A number of studies have reported that a reduction in daylength can stimulate

249   precocious maturation in 0+ parr (Duston and Saunders, 1992; King et al., 2003; Berrill et al.,

250   2003; 2006; Nordgarden et al., 2007). The reduction in growth rate of maturing males in

251   June–July, which is probably concurrent with gonadal development, is also in agreement with

252   other reports on hatchery-reared (Saunders et al., 1982; Rowe and Thorpe, 1990; Foote et al.,

253   1991; Berglund, 1992; Herbinger and Friars, 1992) and wild parr (Whalen and Parrish, 1999).

254   We observed that the effect of a daylength reduction was greatest in the early season in May,

255   intermediate in June, and still positive but statistically not significant in July.

256   Our results support the hypothesis that there is a critical size below which maturation

257   decision remains plastic and responsive to photoperiod manipulation. In early season in May,

258   all individuals appeared to be under this threshold because no length-dependent response to

259   daylength reduction could be detected at that time. This suggests a threshold that is larger

260   than the largest male parr in our study at that time, which was approximately 85 mm. In

261 contrast, a clear threshold appeared for daylength reduction in June and July, being

262 approximately 90 and 100 mm in length, respectively.

263   We estimated length-dependent maturation probabilities using generalized mixed

264 linear models. Our estimations can therefore be interpreted as probabilistic maturation

265 reaction norms (Heino et al. 2002) that have proven to be a useful tool to describe the

266 relationship between the probability of maturation and body size, age, and other explanatory

267 variables, primarily in marine fishes (Dieckmann and Heino, 2007; Heino and Dieckmann

268 2008). Probabilistic maturation reaction norms have also been used to describe the tendency

269 for precocious maturation in salmonids (Piché et al., 2008; Morita et al., 2009). A difference

270 is that most earlier studies have found maturation probabilities to increase with length,

271 whereas the study of Duston et al. (2005) and our results show the opposite, possibly because

272 our experiment described the upper region of the size interval were precocious maturation

273 may be stimulated.

274   The length-dependence of the probability of onset of precocious maturity has

275 similarities with the formation of bimodality. Both processes are stimulated by reduced

276 photoperiod, they are of crucial importance for the further developmental pathway of the fish,

277 and they appear to start at similar fish sizes. Length differences within a narrow range from

278 70 to 80 mm have been of importance for the development of bimodality in several studies

279 (Skilbrei, 1991; Skilbrei and Hansen, 2004; Skilbrei et al., 2007). Assuming a threshold

280 length of approximately 75 mm, the larger fish continued to grow and developed into the

281 upper modal group which smolted in the following spring, while the smaller fish formed the

282 lower modal group, probably because they respond with reduced appetite and growth

283 (Metcalfe et al., 1988). In support of this, Nordgarden et al. (2007) observed a lack of

284 photostimulated plasma growth hormone in 0+ parr smaller than 80 mm and hypothesized

285 that there is a threshold developmental stage at approximately that size that must be reached

286   for the following parr–smolt transformation to be successful. The effect on even smaller fish

287   was not investigated, but our finding that parr of 65–90 mm length are more likely to initiate

288   maturation if day length is reduced, indicates that the physiological decision to initiate the

289   maturation process following a reduction in photoperiod was made in fish belonging to a

290   broader length interval, but one that overlaps with that known to influence the development

291   of bimodality.

292   Observations that wild maturing or mature male parr are of intermediate size relative

293   to the two modal groups (Bagliniere and Maisse, 1985; Presa et al., 1996; Utrilla and Lobón-

294   Cerviá, 1999) support the possibility that the three alternative physiological decisions; to

295   reduce growth (lower-mode fish), increase growth (upper-mode group) or start sexual

296   maturation, are made within the same size interval, at least in cultured fish and possibly also

297   in rapidly growing wild populations. The decisions, to prepare for future smoltification or to

298   mature sexually, are seasonal events that are probably separated by several months in the

299   wild (Letcher and Gries, 2003). When using photoperiod manipulation to produce 0+ smolts,

300   it is possible that both processes are influenced almost simultaneously, and that fish of the

301   same size can develop in different directions.

302   The observation that the future 0+ mature males were smaller than the immature

303   males at the time when the maturation was triggered contrasts with studies on older fish that

304   have shown that the wild (Aubin-Horth and Dodson, 2004) or cultured mature male were

305   larger than future immature fish of the same cohort prior to the onset of maturity (Rowe and

306   Thorpe, 1990; Berglund, 1992; Simpson, 1992; Berrill et al., 2006). Saunders et al. (1982), on

307   the other hand, reported that 1+ male parr that matured were originally the same size as

308   immature fish, and Berglund (1995) reported that although a high growth rate in June

309   stimulated sexual maturity, it was not necessary for the onset of rapid gonadal growth in early

310   summer. Condition factor was similar between the future and immature males in spring, and

311 then increased in maturing male parr during late summer, which is in agreement with several

312 other studies on 0+ (Duston et al., 2005) and 1+ parr (e.g. Berglund, 1992; Rowe and Thorpe,

313 1990).

314   Relationships between fish size and life-history alternatives have also been stressed in

315 studies on precocious maturation in wild salmon. Leonardsson and Lundberg (1986) call

316 attention to the rather narrow range of sizes of mature male parr, and put forward a size-

317 interval hypothesis that would be important for the stability of different life-history strategies

318 in salmon. Several authors have suggested that wild parr must reach a genetically defined

319 threshold level or size to mature. In some comparisons between river sites and river

320 populations, the assumed threshold levels and incidences of mature male parr appear to be

321 correlated with opportunities for growth, while some results can be explained by adaptive

322 mechanisms, and other comparisons show a wide variability that demonstrates that there is a

323 high level of complexity in the proximate mechanisms governing life-history strategies in

324 salmon (Aubin-Horth and Dodson, 2004; Aubin-Horth et al. 2006; Baum et al., 2004; 2005).

325   In conclusion, intensively reared parr of 60–90 mm in length appear to be especially

326 sensitive to photoperiod manipulations that may influence their probability of adopting one of

327 the three life-history alternatives, to enter lower or upper mode or to mature precociously.

328 The physiological and hormonal basis for the developmental thresholds involved, and the

329 roles of genes and their regulation and expression during this sensitive phase, are not known,

330 but should be targeted in future studies in order to improve our understanding of the

331 interactions that take place between the developmental pathways of the individual and its

332 environment.

333

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335

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508 Table 1. Percentages of mature males among all males, and percentages of lower mode fish

509 among females and immature males in PIT-tagged and fin-clipped groups.

510

Photoperiod	Precocious mature males (%)				Lower mode (%)	
	Family A	Family B	Family C	Mean	Mean	
					PIT	Fin
PR-May	41.1	20.2	4.2	21.2	17.0	10.2
PR-June	28.4	14.3	2.8	15.2	5.9	4.8
PR-July	21.4	9.3	0.0	9.2	5.7	5.8
P24	18.0	13.1	0.0	9.6	1.2	0.7
Mean	28.3	14.4	1.8	14.2	7.3	5.2

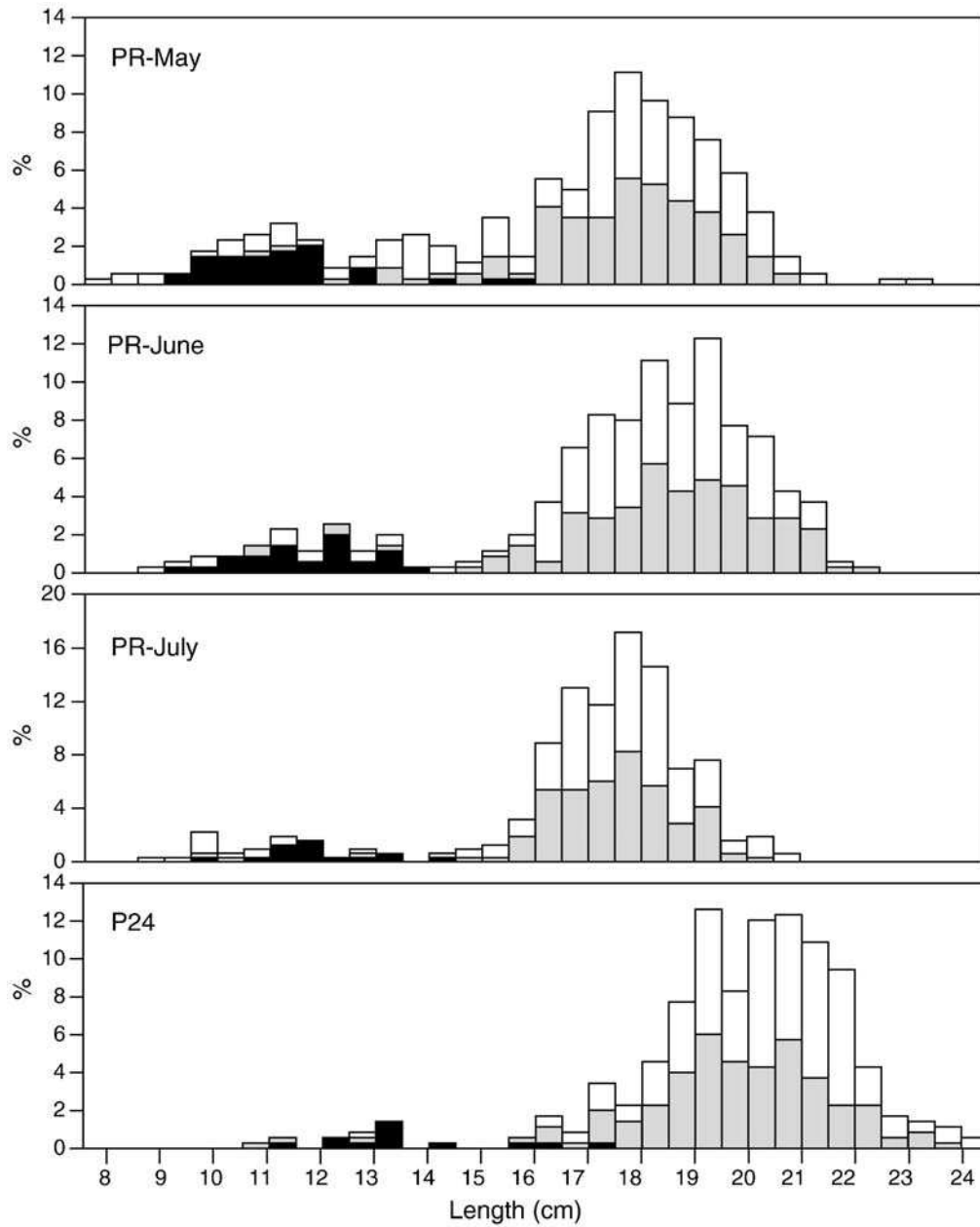511 / 512 / 513 / 514 / 515 / 516 / 517 / 518 / 519 / 520 / 521

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524 Table 2: Summary of multiple analyses of variance in length, condition factor and specific

525 growth rate of immature and maturing males of families A and B testing the effects of parr

526 maturity and the photoperiods employed at different periods from May to November.

527

Dependent Variable	Independent Variables					
	Maturation (M)		Photoperiod (P)		MxP Interaction	
	F	*p*-level	F	p-level	F	*p*-level
Length May	40.3	<0.0001	0.3	0.817	0.2	0.919
Length June	130.5	<0.0001	2.0	0.115	0.9	0.459
Length July	161.1	<0.0001	14.7	<0.0001	3.4	<0.05
Length Sept	477.3	<0.0001	19.8	<0.0001	0.9	0.429
Length Nov	603.2	<0.0001	20.8	<0.0001	4.2	<0.01
SGR May-June	100.3	<0.0001	5.3	<0.05	2.1	0.105
SGR June-July	20.6	<0.0001	45.2	<0.0001	4.3	<0.01
SGR July-Sept	177.7	<0.0001	15.3	<0.0001	0.7	0.521
SGR Sept-Nov	51.1	<0.0001	11.8	<0.0001	0.5	0.655
Cond.f. May	1.0	0.321	2.0	0.107	0.1	0.972
Cond.f. June	5.3	<0.05	2.0	0.120	1.7	0.164
Cond.f. July	5.1	<0.05	28.0	<0.0001	1.7	0.160
Cond.f. Sept	62.2	<0.0001	3.6	<0.05	6.5	<0.001
Cond.f. Nov	73.5	<0.0001	17.7	<0.0001	10.8	<0.0001

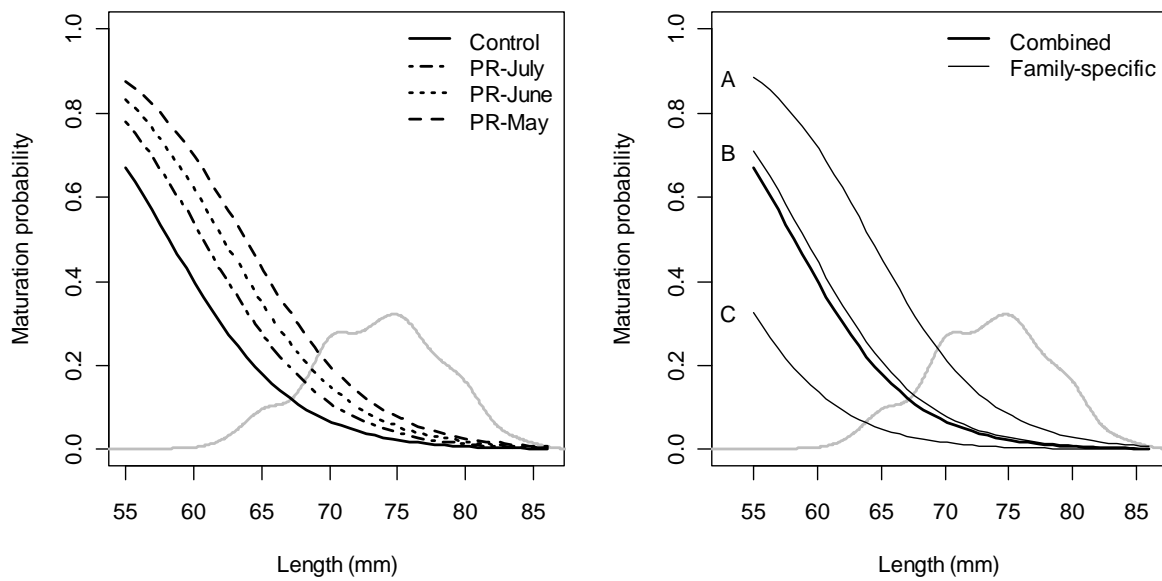528 530 532 534 535 536 537 538 539 540 541 542 543 544 545 546 547 548

549 Figures

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551 Figure 1. Length-frequency distributions of PIT-tagged mature male parr (black bars),

552 immature males (grey bars) and females (white bars) in each of the four treatment groups on

553 24-26 November.

554

555

556 Figure 2. Probabilistic reaction norms for precocious male maturation. Reduced daylength

557 facilitates maturation relative to the control treatment with continuous daylight (left).

558 Maturation tendency varies between families (A, B, and C), here illustrated for the fish in the

559 control treatment (right). Grey lines show the length distribution of all fish in the experiment

560 in May.

May

June

July

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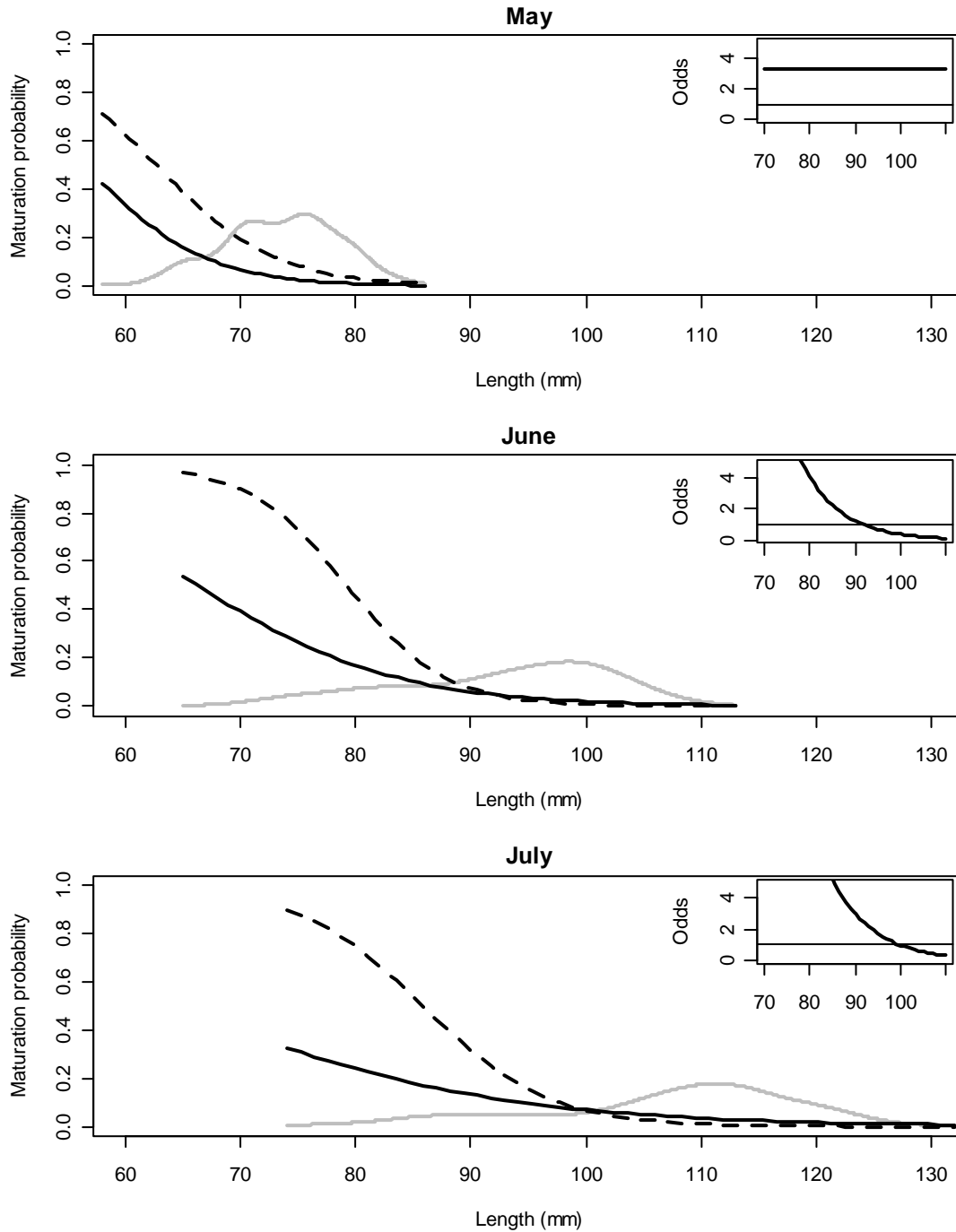
Figure 3. The influence of reducing daylength at different times on the relationship between

precocious male maturation and body length at the time. Continuous black lines show length-

dependent maturation probabilities for control fish, whereas dashed black lines show them for

the fish that were subjected to reduced daylength in a given month. Grey lines show the

combined length distributions for control and treatment fish. Insets show the odds ratios for

maturation in treatment fish relative to control fish. Odds ratios illustrate relative probabilities

568 and make it easier to see whether the change in maturation tendency is length-dependent. In

569 the upper panel, the horizontal line in the inset shows that the daylight reduction facilitated

570 maturation in a length-independent way. In the other two panels, the effect is length-

571 dependent; when the odds ratio is less than one, the daylight reduction is estimated to have

572 inhibited maturation.
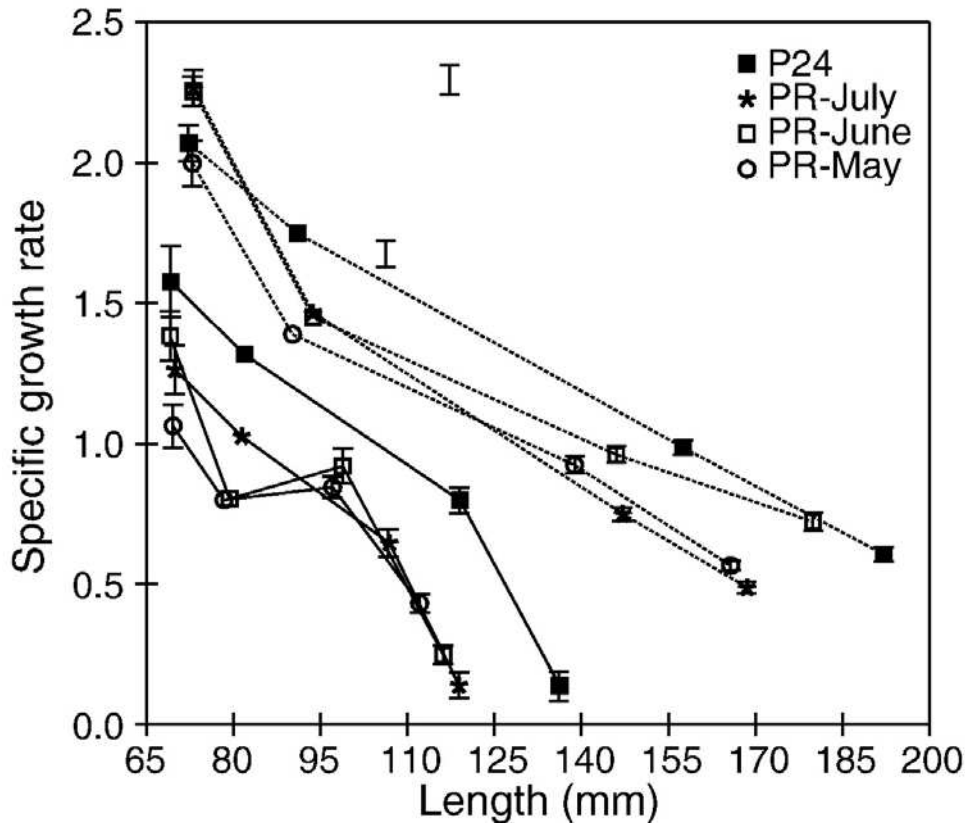
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574 Figure 4. Specific growth rates of the mature (solid lines) and immature males (dashed lines)

575 of Families A and B in the treatment groups throughout the experiment. Means and standard

576 errors are shown. For each group, the four symbols connected with a line correspond from

577 left with the four periods from May to June, June to July, July to October and from October

578 to November.
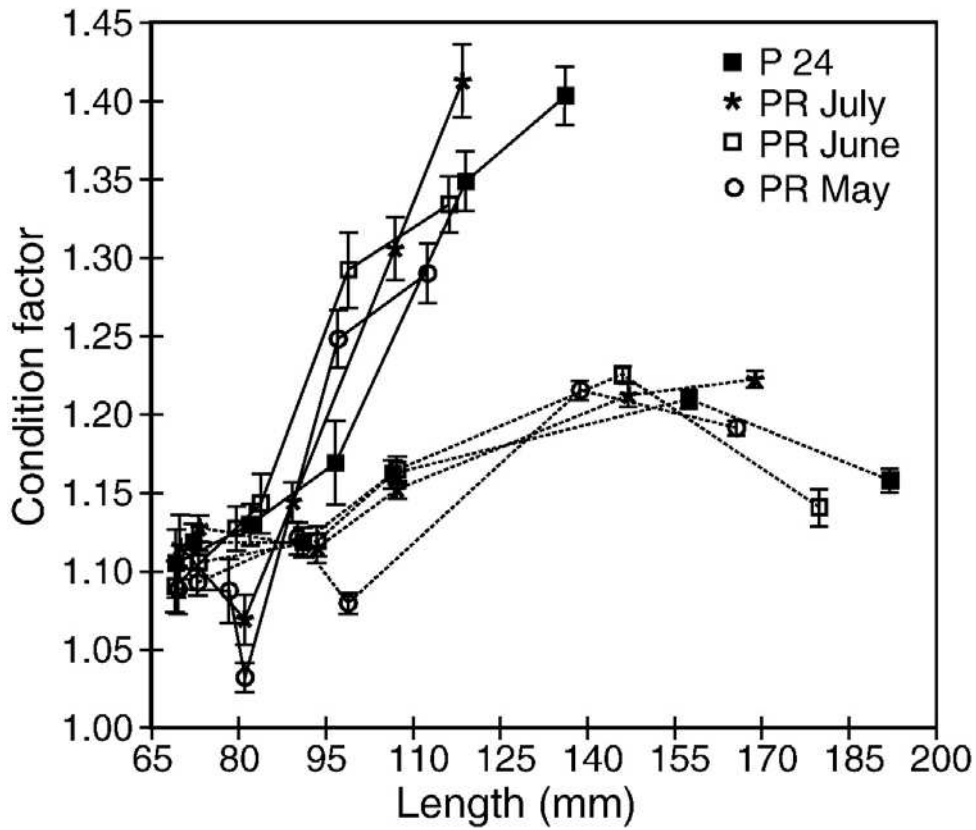
Figure 5. Development in condition factor of the mature (solid lines) and immature males (dashed lines) of Families A and B in the treatment groups from May to November. Means and standard errors are shown. For each group, the five symbols connected with a line correspond from left with the five measurements in May, June, July, September/October and November.

585   Appendix A. Supplementary table and figures

586   Table A1. Explaining maturity in the end of the experiment with size measurements in May

587   and the daylight treatment. Family is treated as a random effect and is present in all models.

588   Because of few missing weight measurements, sample sizes may differ depending on whether

589   body size is measured by length or weight. Akaike Information Criterion (AIC) describes the

590   model fit; among comparable models, the one with the lowest AIC is the best. P values are

591   for likelihood ratio tests comparing simpler models nested within the complex model on the

592   top row; the final model choice among nested models was based on this test rather than AIC.

593

All treatments	Length ($n = 665$)		Weight ($n = 662$)		
Linear predictor	AIC	*P*	AIC	*P*	d.f.
Size+Light+Family	425.45		426.59		
Light+Family	484.53	<0.0001	483.71	<0.0001	1
Size+Family	431.74	0.0065	430.17	0.0225	3

Daylength reduction in May versus control	Length ($n = 337$)		Weight ($n = 336$)		
Linear predictor	AIC	*P*	AIC	P	d.f.
Size*Light+Family	224.62		225.41		
Size+Light+Family	225.63	0.3204	226.72	0.4071	1

Daylength reduction in June versus control	Length ($n = 335$)		Weight ($n = 334$)		
Linear predictor	AIC	*P*	AIC	*P*	d.f.
Size*Light+Family	171.55		173.38		
Size+Light+Family	174.47	0.0266	175.55	0.0412	1

| *Daylength reduction in July versus control*	Length ($n = 304$)		Weight ($n = 304$)		
Linear predictor	AIC	*P*	AIC	*P*	d.f.
Size*Light+Family	137.78		138.58		
Size+Light+Family	142.03	0.0124	144.91	0.0039	1

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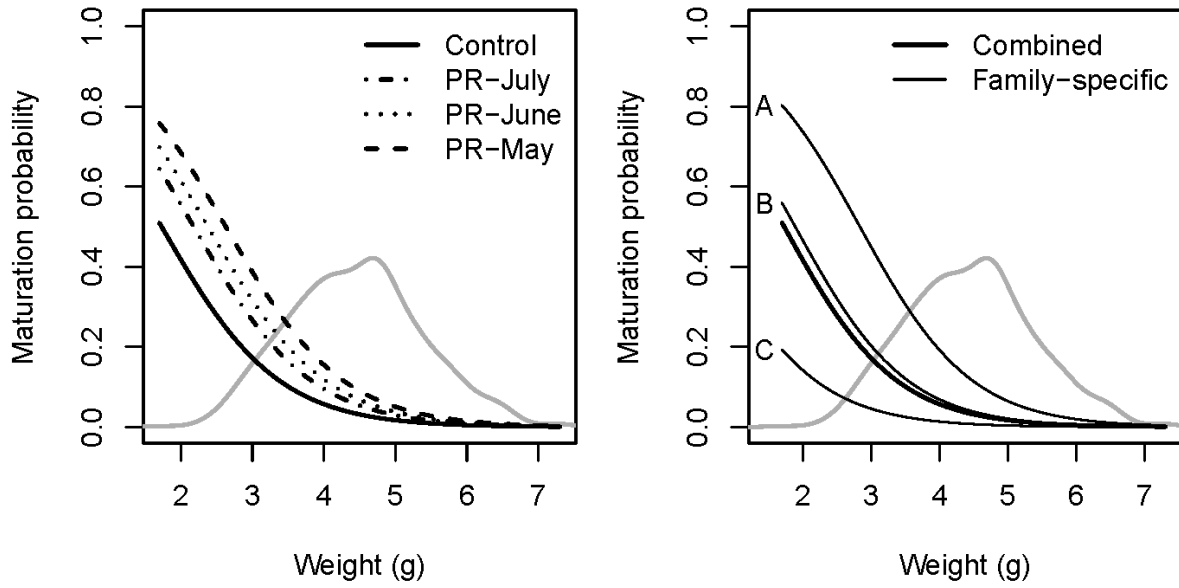
Figure A1. Probabilistic reaction norms for precocious male maturation. Maturation

probability is here expressed as a function of body weight, as opposed to body length used in

Figure 2. For other details, see Figure 2 in the main article.
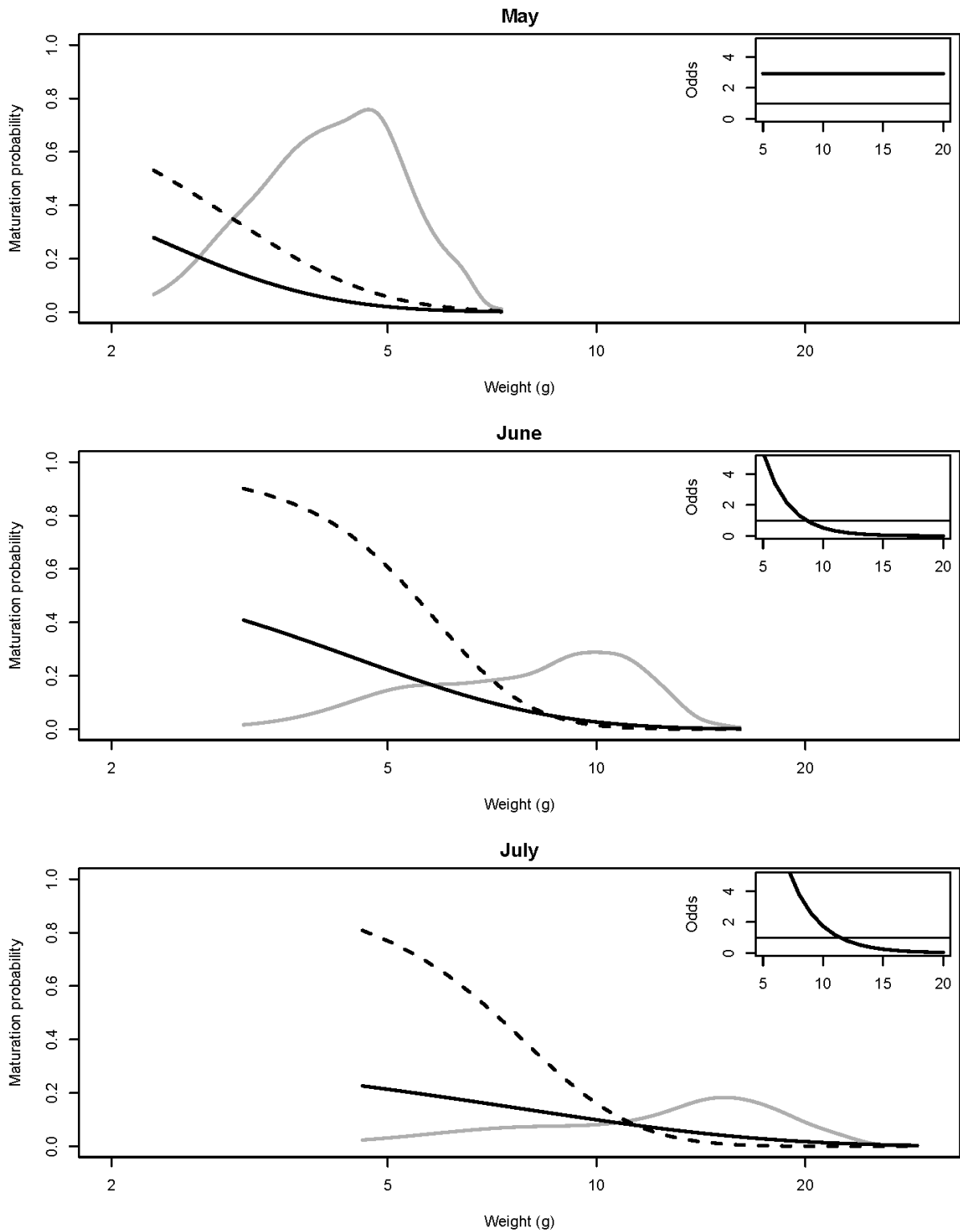
Figure A2. The influence of reducing daylength at different times on the relationship between precocious male maturation and body weight at the time. The figure is similar to Figure 3 in the main article except that body size is here measured as weight instead of length; notice the logarithmic scale on the horizontal axis. For other details, see Figure 3 in the main article.

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