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Reduced daylength stimulates size-dependent precocious maturity in 0+ male Atlantic salmon parr

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1 **Reduced daylength stimulates size-dependent precocious maturity in 0+**
2 **male Atlantic salmon parr**

3

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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 ($\Delta AIC \sim 1$ 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:

$$139 \text{ SGR (\% d}^{-1}\text{)} = 100 \times (\ln(W_2) - \ln(W_1)) / (t_2 - t_1),$$

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

$$141 C = 100 \times W_1 / L_1^3$$

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 $p_{\text{treatment}}, p_{\text{family}} < 0.0001$). There were no significant contributions from rearing the fish in
158 parallel tanks in either model ($p_{\text{tank}} = 0.70$ 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 ($p_{\text{Mark}} = 0.96$), and close to significance for the lower mode fish ($p_{\text{Mark}} = 0.053$). 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

188 *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

199 *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 \pm 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 where 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 (Metcalf 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

511 Photoperiod	511 Precocious mature males (%)				511 Lower mode (%)		
512	<hr/>				<hr/>		
513	Family A	Family B	Family C	Mean	513 Mean		
514					514 PIT	514 Fin	
515	<hr/>						
516	PR-May	41.1	20.2	4.2	21.2	17.0	10.2
517	PR-June	28.4	14.3	2.8	15.2	5.9	4.8
518	PR-July	21.4	9.3	0.0	9.2	5.7	5.8
519	P24	18.0	13.1	0.0	9.6	1.2	0.7
520	Mean	28.3	14.4	1.8	14.2	7.3	5.2
521	<hr/>						

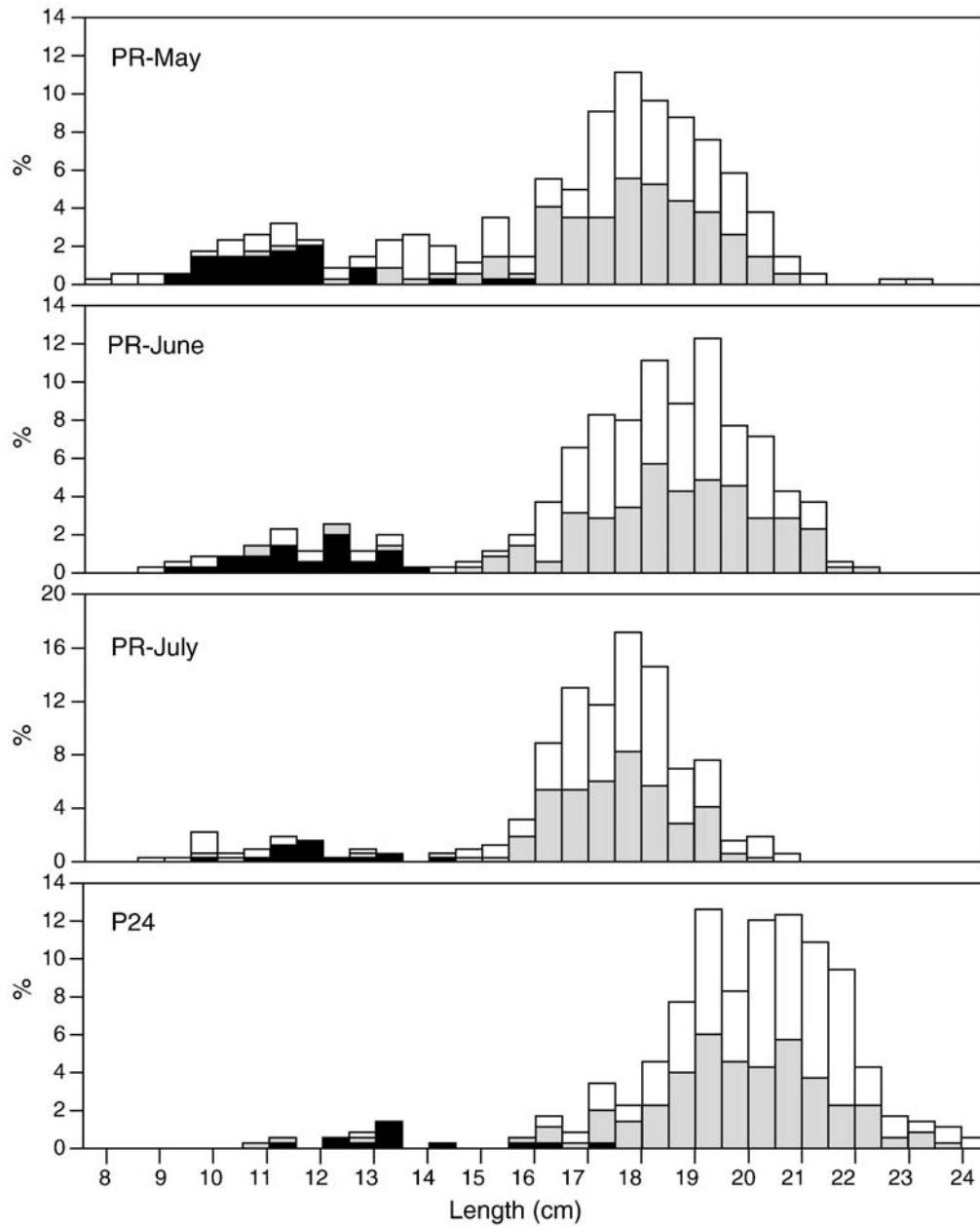
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524 Table 2: Summary of multiple analyses of variance in length, condition factor and specific
 525 growth rate of immature and maturing males of families A and B testing the effects of parr
 526 maturity and the photoperiods employed at different periods from May to November.

528 Dependent 529 Variable	Independent Variables					
	Maturation (M)		Photoperiod (P)		MxP Interaction	
	F	<i>p</i> -level	F	<i>p</i> -level	F	<i>p</i> -level
534 Length May	40.3	<0.0001	0.3	0.817	0.2	0.919
535 Length June	130.5	<0.0001	2.0	0.115	0.9	0.459
536 Length July	161.1	<0.0001	14.7	<0.0001	3.4	<0.05
537 Length Sept	477.3	<0.0001	19.8	<0.0001	0.9	0.429
538 Length Nov	603.2	<0.0001	20.8	<0.0001	4.2	<0.01
539 SGR May-June	100.3	<0.0001	5.3	<0.05	2.1	0.105
540 SGR June-July	20.6	<0.0001	45.2	<0.0001	4.3	<0.01
541 SGR July-Sept	177.7	<0.0001	15.3	<0.0001	0.7	0.521
542 SGR Sept-Nov	51.1	<0.0001	11.8	<0.0001	0.5	0.655
543 Cond.f. May	1.0	0.321	2.0	0.107	0.1	0.972
544 Cond.f. June	5.3	<0.05	2.0	0.120	1.7	0.164
545 Cond.f. July	5.1	<0.05	28.0	<0.0001	1.7	0.160
546 Cond.f. Sept	62.2	<0.0001	3.6	<0.05	6.5	<0.001
547 Cond.f. Nov	73.5	<0.0001	17.7	<0.0001	10.8	<0.0001

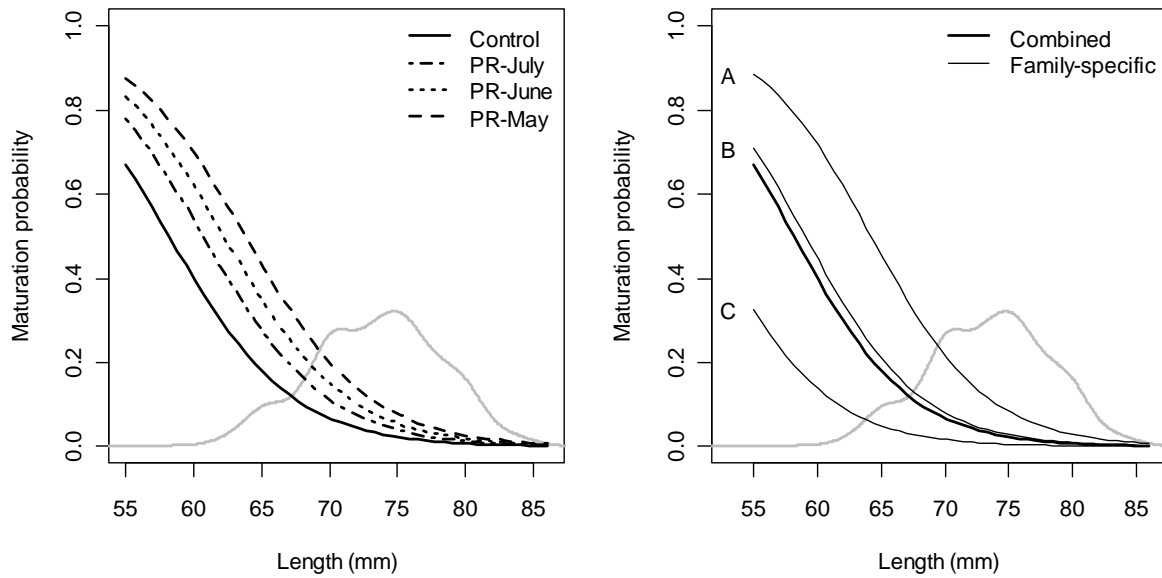
549 Figures



550

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.

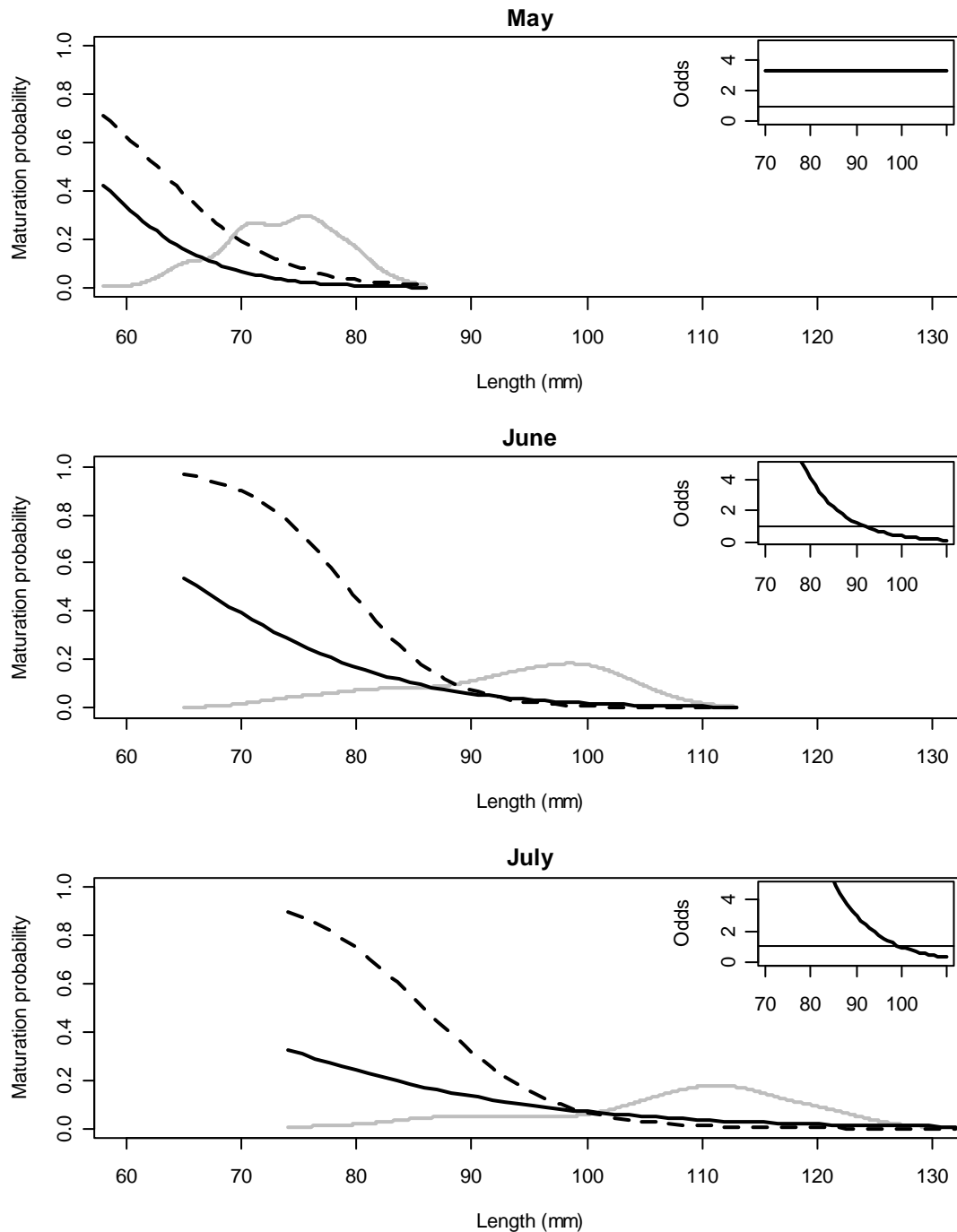
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555

556 Figure 2. Probabilistic reaction norms for precocious male maturation. Reduced daylength
 557 facilitates maturation relative to the control treatment with continuous daylight (left).

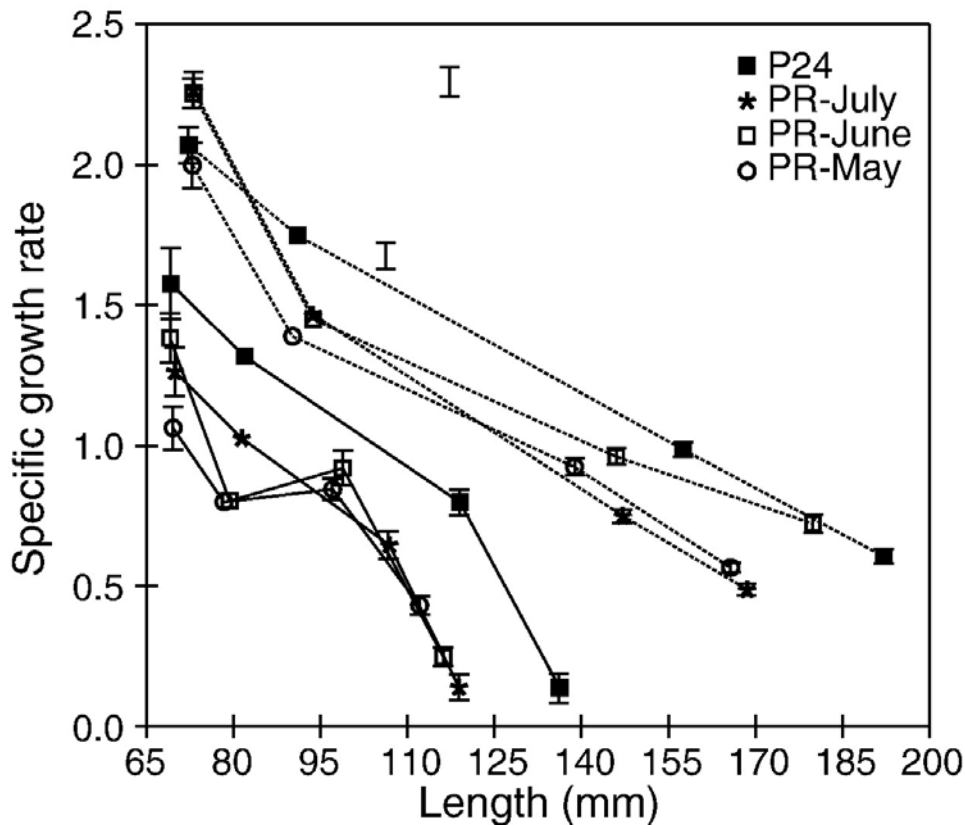
558 Maturation tendency varies between families (A, B, and C), here illustrated for the fish in the
 559 control treatment (right). Grey lines show the length distribution of all fish in the experiment
 560 in May.



561

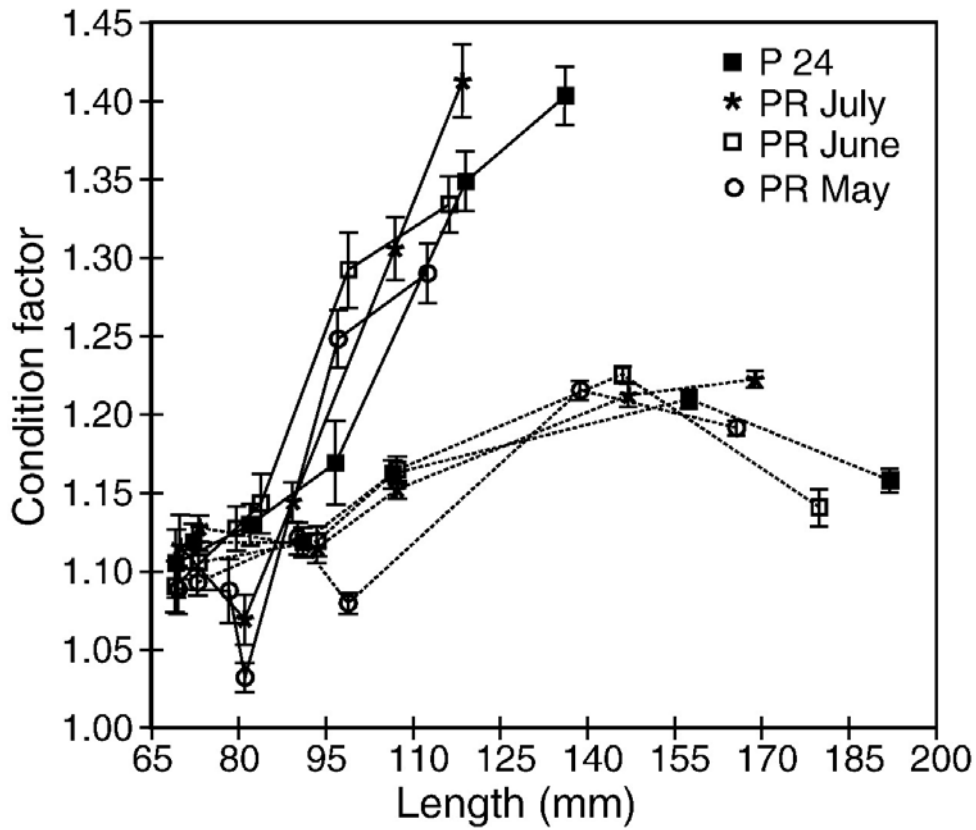
562 Figure 3. The influence of reducing daylength at different times on the relationship between
 563 precocious male maturation and body length at the time. Continuous black lines show length-
 564 dependent maturation probabilities for control fish, whereas dashed black lines show them for
 565 the fish that were subjected to reduced daylength in a given month. Grey lines show the
 566 combined length distributions for control and treatment fish. Insets show the odds ratios for
 567 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.



573

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.



579

580 Figure 5. Development in condition factor of the mature (solid lines) and immature males

581 (dashed lines) of Families A and B in the treatment groups from May to November. Means

582 and standard errors are shown. For each group, the five symbols connected with a line

583 correspond from left with the five measurements in May, June, July, September/October and

584 November.

585 Appendix A. Supplementary table and figures

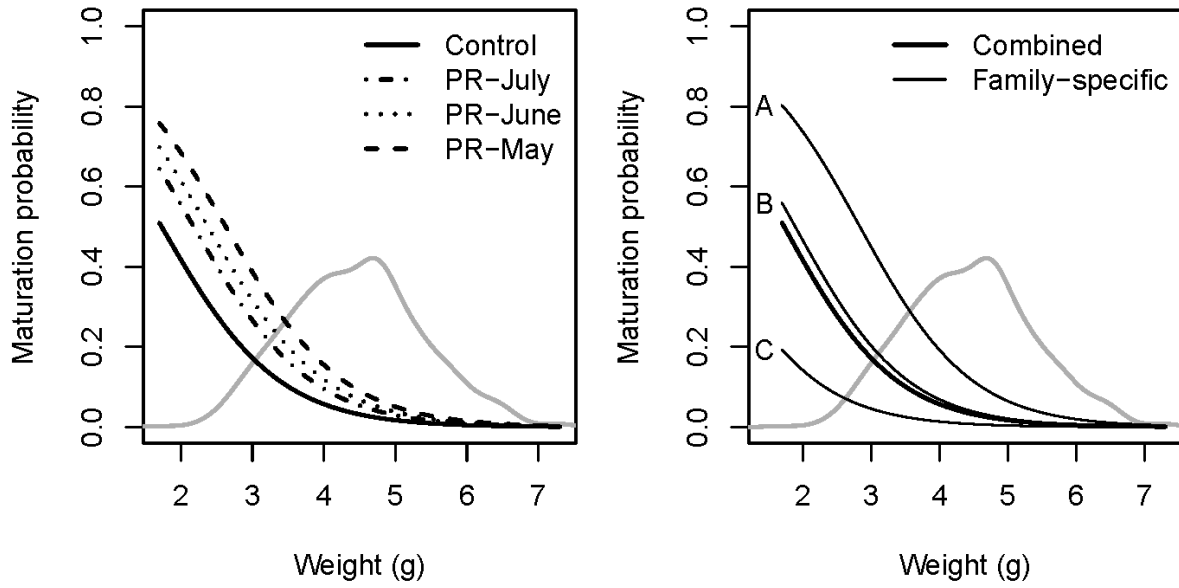
586 Table A1. Explaining maturity in the end of the experiment with size measurements in May
 587 and the daylight treatment. Family is treated as a random effect and is present in all models.
 588 Because of few missing weight measurements, sample sizes may differ depending on whether
 589 body size 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

<i>All treatments</i>					
Linear predictor	Length (<i>n</i> = 665)		Weight (<i>n</i> = 662)		d.f.
	AIC	<i>P</i>	AIC	<i>P</i>	
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
<i>Daylength reduction in May versus control</i>					
Linear predictor	Length (<i>n</i> = 337)		Weight (<i>n</i> = 336)		d.f.
	AIC	<i>P</i>	AIC	<i>P</i>	
Size*Light+Family	224.62		225.41		
Size+Light+Family	225.63	0.3204	226.72	0.4071	1
<i>Daylength reduction in June versus control</i>					
Linear predictor	Length (<i>n</i> = 335)		Weight (<i>n</i> = 334)		d.f.
	AIC	<i>P</i>	AIC	<i>P</i>	
Size*Light+Family	171.55		173.38		
Size+Light+Family	174.47	0.0266	175.55	0.0412	1
<i>Daylength reduction in July versus control</i>					
Linear predictor	Length (<i>n</i> = 304)		Weight (<i>n</i> = 304)		d.f.
	AIC	<i>P</i>	AIC	<i>P</i>	
Size*Light+Family	137.78		138.58		
Size+Light+Family	142.03	0.0124	144.91	0.0039	1

594

595

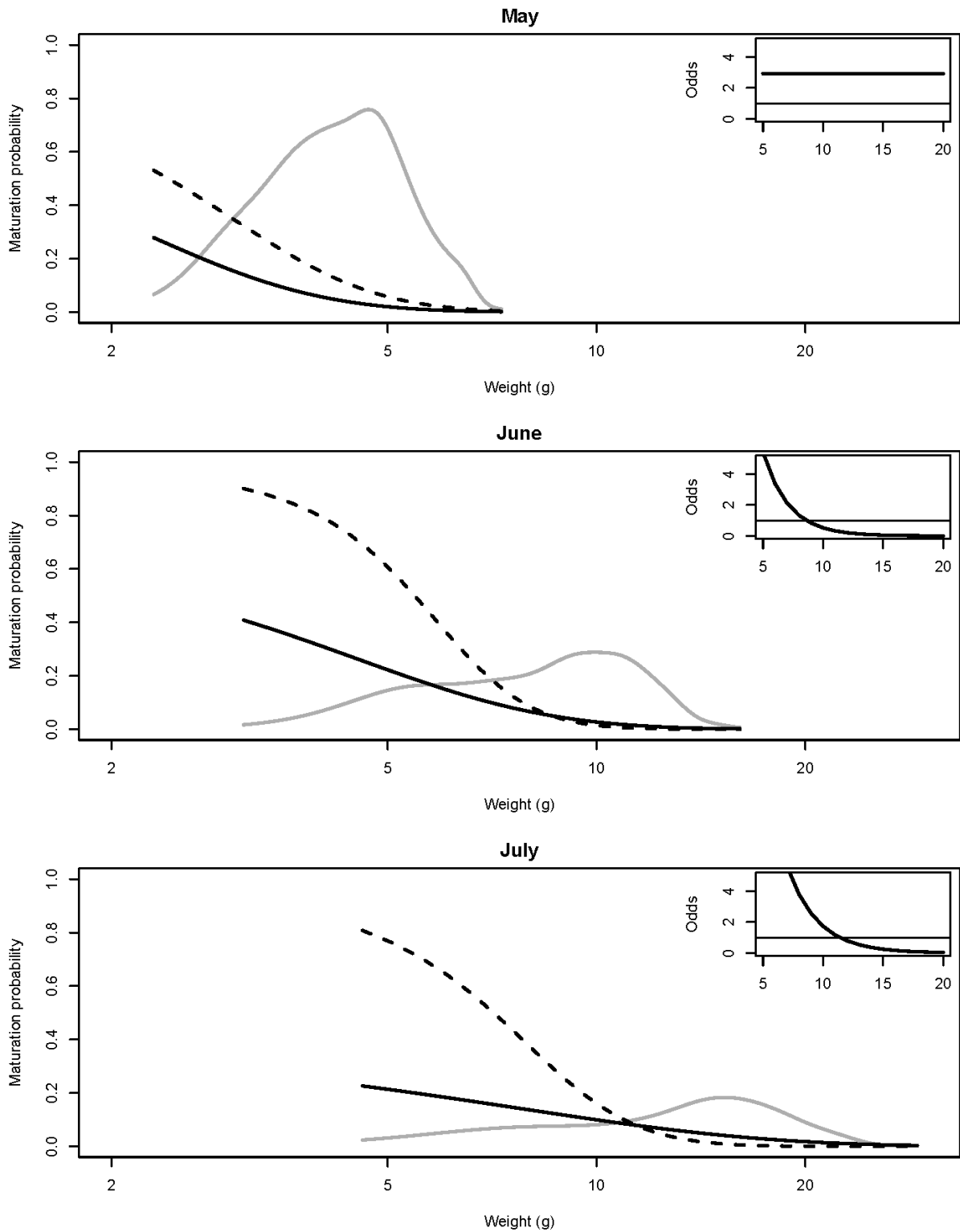


596

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

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

599 Figure 2. For other details, see Figure 2 in the main article.



600

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

605

606