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Reduced daylength stimulates size-dependent precocious maturity in 0+ male Atlantic salmon parr
Ove T. Skilbrei (ove.skilbrei@imr.no)
Mikko Heino (mikko.heino@imr.no)

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

Ove T. Skilbreia* and Mikko Heinoabc

aInstitute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway.
bDepartment of Biology, University of Bergen, Box 7803, N-5020 Bergen, Norway
cEvolution and Ecology Program, International Institute for Applied Systems Analysis (IIASA), A-2361 Laxenburg, Austria

*Corresponding author, Tel.: +47 55236894; fax: +47 55 23 85 31 Email address: ove.skilbrei@imr.no

Abstract
To study relationships between fish length, photoperiod and the onset of precocious maturity in 0+ parr during intensive rearing of Atlantic salmon (Salmo salar L.), 0+ juveniles of 62–82 mm length were individually tagged with Passive Induced Transponders (PITs) in May and exposed to reduced daylength (LD12:12) in May, June or July, or kept as control fish under continuous light. Relationships between the length of the fish and maturity were studied by the use of probabilistic maturation reaction norms. The incidence of mature males and the proportion of fish of lower modal group size in autumn were highest in the groups exposed to short days in May, and lowest under continuous light. In contrast with the expectation that high growth rates promote maturation, the future mature male parr were smaller than the immature males at the start of the experiment, and they also grew more slowly during the subsequent maturation process. Variability in condition factor was low until autumn, when
the condition factor of maturing males rose well above that of immature males during autumn as the fish grew from ~ 80 to ~ 95 mm length. Reduced daylength increased the probability of the onset of precocious maturity in the fish smaller than, but not above a threshold length of ~ 90–100 mm (9–11 g). Intensively reared parr of 60–90 mm, and possibly also smaller fish, may be particularly sensitive to photoperiod manipulations that may influence the probabilities of fish adopting one of the three life-history alternatives, to enter lower or upper mode or to mature precociously.

Key words: Mature male parr, threshold length, probabilistic maturation reaction norms, fish culture, growth, bimodality

1. Introduction

The high degree of adaptive flexibility displayed by Atlantic salmon (Salmo salar L.) is exemplified by the existence of a life-history strategy that includes a reproductive cycle in male parr while they still live in freshwater. It is generally accepted for many fish species that growth rate is positively correlated with an increased probability of maturation (Alm, 1959; Taranger et al., 2010), and improved conditions for growth increase the proportion of mature male parr in hatcheries (Leyzerovich, 1973). Experiments with 1+ juvenile salmon have confirmed that rapid growth may result in early maturation in male parr (e.g. Rowe and Thorpe 1990; Berglund 1992). Condition factor in spring has also been positively related to the incidence of maturation in 1+ parr (Saunders and Duston 1997), but not in 0+ parr (Duston et al. 2005).

Precocious maturation represents a production loss in commercial hatchery production due to reduced growth and negative interference with smoltification (Thorpe and Morgan, 1980;
The introduction of more intensive rearing methods implementing increased temperature and photoperiod manipulations to produce underyearling smolts has also accelerated the developmental rates of parr that mature precociously. Rearing protocols normally involve the fish being first fed under continuous light, after which the photoperiod is reduced during the summer before being raised again in autumn to synchronize the smoltification process (Saunders et al. 1990; Berge et al. 1995; Duston and Saunders 1995). The use of short daylengths during the first summer has been shown to stimulate precocious maturation to various degrees, depending on the timing and duration of the short day treatment (Duston and Saunders, 1992; King et al., 2003; Berrill et al., 2003; 2006; Nordgarden et al., 2007).

The relationships between growth rate, fish size and probability of precocious maturation are complex, because of the dynamic growth pattern that salmon in culture display. This often produces a bimodal length-frequency distribution during their first year of life, with an upper mode of smolts and a lower mode of more slowly developing parr (Thorpe, 1977; Kristinsson et al., 1985; Skilbrei, 1988). It is not clear to what extent the onset of precocious maturation is directly related to size, or to the two alternative developmental routes of the lower and upper mode fish. Studies of threshold sizes for parr maturation have usually described size variation among wild sexually mature parr (Aubin-Horth and Dodson, 2004; Baum et al., 2004, 2005). However, the correlation between the size of the male at the onset of maturity, and its size when it is sexually mature, probably varies greatly with the opportunities for growth experienced by the fish during the maturation process.

There is a lack of more detailed information on relationships between fish size, reduction in photoperiod and onset of precocious maturity under intensive rearing conditions. The purpose of the present study was to provide this kind of information, by studying the
response of individually tagged cultured parr that were exposed to a shortened photoperiod at various dates during their first spring and summer under favourable conditions for growth.

2. Materials and Methods

2.1. Fish and experimental treatments

Three family groups that were offspring of 2-sea-winter salmon of the domesticated Aqua Gen strain were used. Eyed eggs were incubated in darkness. The fish were first fed on 5 March and kept under continuous light until the start of the experiment at Matre Research Station. A total of 1500 individuals with a mean length of 74±5 mm, 500 from each family, were tagged with Passive Induced Transponders (PIT) (size: 2x12 mm, Trovan®) in late May. The fish were anaesthetized with benzocain. A small cut was made with a scalpel to insert the tag into the body cavity. The wound was treated with the antibiotic nitrofurazone to prevent bacterial infections. The fish were distributed equally into eight 1x1 m 300 l square tanks (187–188 individuals per tank). These tanks were the experimental units, whereas the observational unit was a single fish.

To check whether the PIT tags affected the development of the fish, a further 70 fish from each of the three families were fin-clipped differently (unclipped and left and right pelvic fin) and supplied to each tank. To reduce the density of fish in the tanks, the numbers were reduced to ~ 50 fish per family per tank on 29 September. Due to mortality in one tank after one week (25 % of fish), and rejections of individual data points due to error readings (of tag code, length or weight), 1360 individually tagged fish and 1013 fin-clipped fish were finally used for analysis.
The fish were tagged on 21–23 May. Length and size were also measured on 23–25 June, 15–22 July, 30 Sept–2 Oct, on 24–26 November and finally on 19 January when all the fish were killed and gonads examined. The fish were held under continuous light from first feeding until the start of the experiment. Photoperiod was reduced to 12 hours of daily light in parallel tanks on three successive dates during summer; on 23 May, on 25 June and on 22 July, while controls were kept under continuous light (PR-May, PR-June, PR-July and P24). The fish were held under these four photoperiods until the end of the experiment. The fish were fed commercial dry pellets by automatic feeders 12 h per day from the start of the experiment in late May.

Mean temperature and monthly means were 13.2 °C from first feeding to the start of the experiment. From June to October, the mean temperature was 12.7 °C, with a variation from 11.5 to 14.1 °C between months. It then declined during autumn to 8.4 °C in November, 6.7 °C in December and 5.8 °C in January.

2.2. Data treatment and statistical analyses

On the basis of inspection of the length-frequency distributions the lower mode fish were defined as those smaller than 145 mm in November (Fig. 1).

The GLM (General Linear Models) module of the statistical package STATISTICA (Statsoft 2008) was applied for one-way and multiple analysis of variance in length, condition factor and specific growth rate in different treatment groups and parallel tanks (as random effect), and for multiple post hoc comparisons to test means of specific groups (Newman-Keuls). The lme4 package by Bates and Mechler (2010) under R 2.11 was used to fit Generalized Linear Mixed Models (GLMM) with a logistic link function to test for
differences in the incidence of mature male parr and for variability in the proportion of lower modal group fish.

In estimating the effects of marking on maturation and probability of being a lower modal group fish, marking method and experimental treatment were treated as fixed effects and family and tank were treated as random effects. In estimating size-dependent maturation probabilities (i.e., probabilistic maturation reaction norms, see Heino et al., 2002), size was a variate, experimental treatment was a fixed effect, and family and tank were random effects. However, because the tank effect was never significant, this effect was not included in any of the final models. Size was measured as both length and weight. Both measures are good predictors of maturation, and our results are qualitatively independent from the choice of size metric. For simplicity, we focus here on length – models using length were slightly better than those using weight (ΔAIC~1 in favour of length). Appendix A gives the main results for both length- and weight-based estimations.

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

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

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

$$C_1 = 100 \times \frac{W_1}{L_1^3}$$

where $L_1$ is fork length in cm.

3. Results

3.1 Proportions of mature male parr and lower modal group fish
The proportions of mature male parr were highest following the reduction in photoperiod in May, and were halved during the subsequent two reductions (Table 1). The control group performed comparably to the PR-July group. The proportion of lower modal group fish declined in a similar way, except that the PR-June and PR-July treatments were almost identical and that P24 contained only one fifteenth of the lower mode fish in PR-May (Table 1). Family A produced the highest proportions of both mature male parr (Table 1) and lower modal group fish among immature fish (15.7% vs 2.5 and 2.0% in Families B and C, respectively). Treatment and family significantly affected both the incidences of mature male parr and the percentages of lower mode fish (both GLMM binomial response models: $p_{\text{treatment}}$, $p_{\text{family}} < 0.0001$). There were no significant contributions from rearing the fish in parallel tanks in either model ($p_{\text{tank}} = 0.70$ and 0.56, respectively). The differences between the groups tagged with PITs or fin-clips were insignificant for the incidence of mature males ($p_{\text{Mark}} = 0.96$), and close to significance for the lower mode fish ($p_{\text{Mark}} = 0.053$). The use of PIT tags therefore appeared to be of minor importance for the development of the fish.

3.2 Length-dependent response to photoperiod

The immature future lower modal group fish of the PR-May treatment had a mean length of $69 \pm 4$ mm in late May, as opposed to $75 \pm 5$ mm of the fish that entered the upper mode (t-test, $p < 0.0001$).

Maturity in the end of the experiment was significantly explained by length in May (likelihood ratio test: d.f.=1, $p<0.0001$), with the probability of maturing being a decreasing function of length (Fig. 2). Reduced daylength resulted in increased tendency to mature (likelihood ratio test: d.f.=3, $p=0.006$). This effect became weaker the later light regime was
manipulated, and the effect was not significant for fish exposed to reduced daylength in July. At the same time, there were large differences between the families (Fig. 2).

Fish that were exposed to reduced daylength in May showed increased maturation tendency relative to the control fish (d.f.=1, p=0.0017), but this increase was length-independent: the interaction between treatment and length was insignificant (d.f.=1, p=0.32) and the odds on maturing in the final model thus length-independent (Fig. 3). However, the fish that were exposed to reduced daylength in June showed a length-dependent response: the model with length-treatment interaction was significantly better than one without (d.f.=1, p=0.027). Fish that were less than about 90 mm in length in June responded to reduced daylength by increasing their maturation tendency, whereas larger fish had an opposite response (Fig. 3). Similar results were obtained for daylength change in July (p=0.012 for the length-treatment interaction), although the threshold below which maturation was facilitated was shifted upwards to around 100 mm. In summary, reduced daylength facilitates maturation, but only so below a threshold of about 90–100 mm. The corresponding thresholds in weight were 7-11 g (see Appendix A; Table A1 and Figs A1 and A2).
3.3 Influence of photoperiod and maturity on growth and condition

Only the maturing and immature males of family A and B were used for further treatment of the data in figures 4 and 5 and statistics shown in Table 2 due to the low incidence of mature male parr in family C. With one exception, the use of parallel tanks did not contribute significantly to any of the multiple analyses of variance in length, condition factor and growth rate, and was not included in the reported models (Table 2). The exception was caused by significant differences in growth rates of the fish in parallel tanks under the PR-June treatment during the two last measurements (p<0.05, Newman-Keuls multiple test).

3.3.1 Size and growth rates of males

The future mature males of family A and B were significantly smaller than the immature males at the start of the experiment in May, 69±4 mm (mean±SD) versus 74±5 (p<0.05, Newman-Keuls tests). These differences in initial length contributed significantly to the multiple analyses of variance, and increased during the experiment because of the clearly higher growth rates of immature fish (Table 2, Fig. 4).

The growth rates of the future mature males dropped shortly after reductions in photoperiod (Fig. 4). The growth rates of PR-May, PR-June and PR-July were significantly lower than the P24 maturing males starting from the first, second and third period of measurement, respectively (p<0.05, Newman-Keuls tests), and as a result, the P24 mature males were significantly larger than the other mature males at the end of the experiment (p<0.05, Newman-Keuls tests). Due to these developmental characteristics, maturity
significantly affected the variability in length and growth rates at all periods. The effect of photoperiod was weaker (lower F values), and did not significantly affect length before the third measurement in July (Table 2). Interactions between maturity and photoperiod were weak in most cases and did not seem to be important for the overall results (Table 2).

3.3.2 Development in condition factor of males

There was no significant variation in condition factor at the start of the experiment between the immature males and the future mature males. Significant effects of either maturity or photoperiod were seen in June and July, but the contributions from both factors to total variability became much clearer during the autumn, when the condition factor of maturing males rose well above that of immature males as the fish grew from ~ 80 to ~ 95 mm length (Table 2, Fig.5). A significant interaction between maturity and photoperiod also developed during the autumn (Table 2), partly because of a negative relationship between the condition factor of maturing males and the duration of the period they had been held under 12 hours of daily light (Condition factor of PR-May < PR-June < PR-July and P24; p<0.05, Newman-Keuls tests).

3.3.3 Growth rates of males in comparison to females

Possibly because of higher probability of maturation in the PR-May treatment group among initially smaller, slow-growing males (see above), the remaining immature males comprised more rapidly growing fish. They grew faster than the females during the first three periods from May to October (mean specific growth rates of immature males and females were
1.59±32 d⁻¹ and 1.44±0.39 d⁻¹ from May to October) and were larger than the females from on June (immature males and females weighted 9.3±0.3 g and 8.5±0.3 g in June, and 39.4±1.4 g and 35.3±1.8 g in early October) (Newman-Keuls tests, p<0.05). Immature males and females of the other treatment groups were not significantly different.

4. Discussion

Reductions in daylength triggered precocious maturation in male parr reared under intensive hatchery conditions, and the growth rates of the maturing males declined shortly after the photoperiod adjustments. This study is the first to demonstrate a clear relationship between the probability of onset of maturity in 0+ male parr and its length when photoperiod was reduced.

A number of studies have reported that a reduction in daylength can stimulate precocious maturation in 0+ parr (Duston and Saunders, 1992; King et al., 2003; Berrill et al., 2003; 2006; Nordgarden et al., 2007). The reduction in growth rate of maturing males in June–July, which is probably concurrent with gonadal development, is also in agreement with other reports on hatchery-reared (Saunders et al., 1982; Rowe and Thorpe, 1990; Foote et al., 1991; Berglund, 1992; Herbinger and Friars, 1992) and wild parr (Whalen and Parrish, 1999). We observed that the effect of a daylength reduction was greatest in the early season in May, intermediate in June, and still positive but statistically not significant in July.

Our results support the hypothesis that there is a critical size below which maturation decision remains plastic and responsive to photoperiod manipulation. In early season in May, all individuals appeared to be under this threshold because no length-dependent response to daylength reduction could be detected at that time. This suggests a threshold that is larger than the largest male parr in our study at that time, which was approximately 85 mm.
contrast, a clear threshold appeared for daylength reduction in June and July, being approximately 90 and 100 mm in length, respectively.

We estimated length-dependent maturation probabilities using generalized mixed linear models. Our estimations can therefore be interpreted as probabilistic maturation reaction norms (Heino et al. 2002) that have proven to be a useful tool to describe the relationship between the probability of maturation and body size, age, and other explanatory variables, primarily in marine fishes (Dieckmann and Heino, 2007; Heino and Dieckmann 2008). Probabilistic maturation reaction norms have also been used to describe the tendency for precocious maturation in salmonids (Piché et al., 2008; Morita et al., 2009). A difference is that most earlier studies have found maturation probabilities to increase with length, whereas the study of Duston et al. (2005) and our results show the opposite, possibly because our experiment described the upper region of the size interval were precocious maturation may be stimulated.

The length-dependence of the probability of onset of precocious maturity has similarities with the formation of bimodality. Both processes are stimulated by reduced photoperiod, they are of crucial importance for the further developmental pathway of the fish, and they appear to start at similar fish sizes. Length differences within a narrow range from 70 to 80 mm have been of importance for the development of bimodality in several studies (Skilbrei, 1991; Skilbrei and Hansen, 2004; Skilbrei et al., 2007). Assuming a threshold length of approximately 75 mm, the larger fish continued to grow and developed into the upper modal group which smolted in the following spring, while the smaller fish formed the lower modal group, probably because they respond with reduced appetite and growth (Metcalfe et al., 1988). In support of this, Nordgarden et al. (2007) observed a lack of photostimulated plasma growth hormone in 0+ parr smaller than 80 mm and hypothesized that there is a threshold developmental stage at approximately that size that must be reached.
for the following parr–smolt transformation to be successful. The effect on even smaller fish was not investigated, but our finding that parr of 65–90 mm length are more likely to initiate maturation if day length is reduced, indicates that the physiological decision to initiate the maturation process following a reduction in photoperiod was made in fish belonging to a broader length interval, but one that overlaps with that known to influence the development of bimodality.

Observations that wild maturing or mature male parr are of intermediate size relative to the two modal groups (Bagliniere and Maisse, 1985; Presa et al., 1996; Utrilla and Lobón-Cerviá, 1999) support the possibility that the three alternative physiological decisions; to reduce growth (lower-mode fish), increase growth (upper-mode group) or start sexual maturation, are made within the same size interval, at least in cultured fish and possibly also in rapidly growing wild populations. The decisions, to prepare for future smoltification or to mature sexually, are seasonal events that are probably separated by several months in the wild (Letcher and Gries, 2003). When using photoperiod manipulation to produce 0+ smolts, it is possible that both processes are influenced almost simultaneously, and that fish of the same size can develop in different directions.

The observation that the future 0+ mature males were smaller than the immature males at the time when the maturation was triggered contrasts with studies on older fish that have shown that the wild (Aubin-Horth and Dodson, 2004) or cultured mature male were larger than future immature fish of the same cohort prior to the onset of maturity (Rowe and Thorpe, 1990; Berglund, 1992; Simpson, 1992; Berrill et al., 2006). Saunders et al. (1982), on the other hand, reported that 1+ male parr that matured were originally the same size as immature fish, and Berglund (1995) reported that although a high growth rate in June stimulated sexual maturity, it was not necessary for the onset of rapid gonadal growth in early summer. Condition factor was similar between the future and immature males in spring, and
then increased in maturing male parr during late summer, which is in agreement with several other studies on 0+ (Duston et al., 2005) and 1+ parr (e.g. Berglund, 1992; Rowe and Thorpe, 1990).

Relationships between fish size and life-history alternatives have also been stressed in studies on precocious maturation in wild salmon. Leonardsson and Lundberg (1986) call attention to the rather narrow range of sizes of mature male parr, and put forward a size-interval hypothesis that would be important for the stability of different life-history strategies in salmon. Several authors have suggested that wild parr must reach a genetically defined threshold level or size to mature. In some comparisons between river sites and river populations, the assumed threshold levels and incidences of mature male parr appear to be correlated with opportunities for growth, while some results can be explained by adaptive mechanisms, and other comparisons show a wide variability that demonstrates that there is a high level of complexity in the proximate mechanisms governing life-history strategies in salmon (Aubin-Horth and Dodson, 2004; Aubin-Horth et al. 2006; Baum et al., 2004; 2005).

In conclusion, intensively reared parr of 60–90 mm in length appear to be especially sensitive to photoperiod manipulations that may influence their probability of adopting one of the three life-history alternatives, to enter lower or upper mode or to mature precociously. The physiological and hormonal basis for the developmental thresholds involved, and the roles of genes and their regulation and expression during this sensitive phase, are not known, but should be targeted in future studies in order to improve our understanding of the interactions that take place between the developmental pathways of the individual and its environment.

Acknowledgements
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References


Rowe, D.K., Thorpe, J.E., 1990b. Suppression of maturation in male Atlantic salmon


StatSoft, Inc. 2008. STATISTICA (data analysis software system), version 8.0.


Table 1. Percentages of mature males among all males, and percentages of lower mode fish among females and immature males in PIT-tagged and fin-clipped groups.

<table>
<thead>
<tr>
<th>Photoperiod</th>
<th>Precocious mature males (%)</th>
<th>Lower mode (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Family A</td>
<td>Family B</td>
</tr>
<tr>
<td>PR-May</td>
<td>41.1</td>
<td>20.2</td>
</tr>
<tr>
<td>PR-June</td>
<td>28.4</td>
<td>14.3</td>
</tr>
<tr>
<td>PR-July</td>
<td>21.4</td>
<td>9.3</td>
</tr>
<tr>
<td>P24</td>
<td>18.0</td>
<td>13.1</td>
</tr>
<tr>
<td>Mean</td>
<td>28.3</td>
<td>14.4</td>
</tr>
</tbody>
</table>
Table 2: Summary of multiple analyses of variance in length, condition factor and specific growth rate of immature and maturing males of families A and B testing the effects of parr maturity and the photoperiods employed at different periods from May to November.

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Independent Variables</th>
<th>Maturation (M)</th>
<th>Photoperiod (P)</th>
<th>MxP Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>p-level</td>
<td>F</td>
</tr>
<tr>
<td>Length May</td>
<td>40.3</td>
<td>&lt;0.0001</td>
<td>0.3</td>
<td>0.817</td>
</tr>
<tr>
<td>Length June</td>
<td>130.5</td>
<td>&lt;0.0001</td>
<td>2.0</td>
<td>0.115</td>
</tr>
<tr>
<td>Length July</td>
<td>161.1</td>
<td>&lt;0.0001</td>
<td>14.7</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Length Sept</td>
<td>477.3</td>
<td>&lt;0.0001</td>
<td>19.8</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Length Nov</td>
<td>603.2</td>
<td>&lt;0.0001</td>
<td>20.8</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>SGR May-June</td>
<td>100.3</td>
<td>&lt;0.0001</td>
<td>5.3</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>SGR June-July</td>
<td>20.6</td>
<td>&lt;0.0001</td>
<td>45.2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>SGR July-Sept</td>
<td>177.7</td>
<td>&lt;0.0001</td>
<td>15.3</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>SGR Sept-Nov</td>
<td>51.1</td>
<td>&lt;0.0001</td>
<td>11.8</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Cond.f. May</td>
<td>1.0</td>
<td>0.321</td>
<td>2.0</td>
<td>0.107</td>
</tr>
<tr>
<td>Cond.f. June</td>
<td>5.3</td>
<td>&lt;0.05</td>
<td>2.0</td>
<td>0.120</td>
</tr>
<tr>
<td>Cond.f. July</td>
<td>5.1</td>
<td>&lt;0.05</td>
<td>28.0</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Cond.f. Sept</td>
<td>62.2</td>
<td>&lt;0.0001</td>
<td>3.6</td>
<td>&lt;0.05</td>
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<tr>
<td>Cond.f. Nov</td>
<td>73.5</td>
<td>&lt;0.0001</td>
<td>17.7</td>
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Figure 1. Length-frequency distributions of PIT-tagged mature male parr (black bars), immature males (grey bars) and females (white bars) in each of the four treatment groups on 24-26 November.
Figure 2. Probabilistic reaction norms for precocious male maturation. Reduced daylength facilitates maturation relative to the control treatment with continuous daylight (left). Maturation tendency varies between families (A, B, and C), here illustrated for the fish in the control treatment (right). Grey lines show the length distribution of all fish in the experiment in May.
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.
and make it easier to see whether the change in maturation tendency is length-dependent. In the upper panel, the horizontal line in the inset shows that the daylight reduction facilitated maturation in a length-independent way. In the other two panels, the effect is length-dependent; when the odds ratio is less than one, the daylight reduction is estimated to have inhibited maturation.

Figure 4. Specific growth rates of the mature (solid lines) and immature males (dashed lines) of Families A and B in the treatment groups throughout the experiment. Means and standard errors are shown. For each group, the four symbols connected with a line correspond from left with the four periods from May to June, June to July, July to October and from October 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.
Appendix A. Supplementary table and figures

Table A1. Explaining maturity in the end of the experiment with size measurements in May and the daylight treatment. Family is treated as a random effect and is present in all models. Because of few missing weight measurements, sample sizes may differ depending on whether body size is measured by length or weight. Akaike Information Criterion (AIC) describes the model fit; among comparable models, the one with the lowest AIC is the best. P values are for likelihood ratio tests comparing simpler models nested within the complex model on the top row; the final model choice among nested models was based on this test rather than AIC.

<table>
<thead>
<tr>
<th>Linear predictor</th>
<th>All treatments</th>
<th>Daylength reduction in May versus control</th>
<th>Daylength reduction in June versus control</th>
<th>Daylength reduction in July versus control</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length (n = 665)</td>
<td>Weight (n = 662)</td>
<td>Length (n = 337)</td>
<td>Weight (n = 335)</td>
</tr>
<tr>
<td></td>
<td>AIC</td>
<td>P</td>
<td>AIC</td>
<td>P</td>
</tr>
<tr>
<td>Size+Light+Family</td>
<td>425.45</td>
<td>426.59</td>
<td>224.62</td>
<td>225.41</td>
</tr>
<tr>
<td>Light+Family</td>
<td>484.53</td>
<td>&lt;0.0001</td>
<td>225.63</td>
<td>0.3204</td>
</tr>
<tr>
<td>Size+Family</td>
<td>431.74</td>
<td>0.0065</td>
<td>226.72</td>
<td>0.4071</td>
</tr>
</tbody>
</table>

AIC describes the model fit; among comparable models, the one with the lowest AIC is the best. P values are for likelihood ratio tests comparing simpler models nested within the complex model on the top row; the final model choice among nested models was based on this test rather than AIC.
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.