Photoperiodic effects on precocious maturation, growth and smoltification in Atlantic salmon, Salmo salar.

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Abstract

Current Atlantic salmon farming practice induces early smoltification with artificial photoperiod regimes, however the importance of these photoperiods on parr maturation and interactions with smoltification are poorly understood. These questions were addressed in the present investigation, which examined the effects of photoperiod manipulation on the development, maturation and smoltification of individually tagged parr.

Approximately 9000 salmon parr from a high grilsing stock were exposed to continuous light (LL) from first feeding. Three sub-groups of 2400 parr, each sub-group in triplicate tanks, were then exposed to an 8 week "winter photoperiod" (LD 10:14) starting on either the 18th May, the 9th August or the 20th September (defined respectively as the May, August and September groups). Following the artificial winter each group was returned to LL. A fourth group of 1600 fish was maintained in replicate tanks on LL throughout.

The highest levels of maturation (approx. 20%) were recorded in the May group. August and September groups showed low levels of maturity (<5%) with constant LL throughout resulting in intermediate levels (<9%). However, only groups exposed to the August photoperiod showed high levels of smoltification.

It is concluded that the photoperiod to which parr are exposed early in their life acts as an important trigger for precocious maturation but does not necessarily phase shift the endogenous rhythm which is thought to control its timing. Smoltification is strongly influenced by the timing of exposure to winter photoperiod with clear evidence indicating that maturation and smoltification are not mutually exclusive processes.

Keywords: Atlantic salmon, parr, maturation, smoltification, photoperiod

1. Introduction

Understanding the plasticity of the Atlantic salmon, Salmo salar, life cycle (Thorpe, 1994a; Fleming, 1998; Metcalfe, 1998) is an important determinant of the success of its culture. Of particular importance to growth and smoltification is the “precocious” maturation of a proportion of parr in fresh water. Early maturation, although rare in females (c.f. Bagliniere and Maisse, 1985; Hindar and Nordland, 1989) is commonplace among males under both wild (Dalley et al., 1983; Myers, 1984; Bagliniere and Maisse, 1985; Whalen and Parrish, 1999) and farmed conditions (Thorpe et al., 1990; Rowe and Thorpe, 1990a; Duston and Saunders, 1992, 1997). However, the environmental, physiological and genetic interactions which result in precocious maturation are poorly understood.

Early maturing fish are initially among the fastest growing individuals within the population (Saunders et al., 1982; Rowe and Thorpe, 1990a). However, somatic growth then decreases in favour of gonadal growth. Population bimodality may occur as a consequence of such growth differentials related to life history strategy (Thorpe, 1977; Bailey et al., 1980; Thorpe et al., 1980; Porter et al., 1998). Various thresholds of size, growth rate and energetic status suggested for smoltification (Elson, 1957; Thorpe et al., 1980) and maturation (Berglund, 1992, Herbinger and Friars, 1992; Whalen and Parish, 1999; Porter et al., 1999) are important in determining when smoltification and maturation are initiated. Thorpe and Morgan (1980) and Thorpe (1986) suggested that smolting and maturation are mutually exclusive and that smoltification is the result of a fish failing to mature (Thorpe, 1994b, Thorpe and Metcalfe, 1998). However, Saunders et al. (1982), Myers (1984), Bagliniere and Maisse (1985) and Kristinsson et al. (1985) have all described mature fish which smolt in the subsequent spring suggesting that the two are not mutually exclusive.

The manipulation of environmental parameters such as temperature (Adams and Thorpe, 1989), photoperiod (Adams and Thorpe, 1989) and feed availability (Rowe et al., 1991; Berglund, 1995) at seasonally critical times, has resulted in reduced parr maturation. Photoperiod manipulation is the tool most used by farms to control growth, reproduction and smoltification (Hansen et al., 1992; Thrush et al., 1994; Duncan et al., 1998; Porter et al., 1999; Endal et al., 2000). However, the effects of photoperiod on parr maturation (e.g. Lundqvist, 1980; Saunders and Henderson, 1988) are still largely unknown and are further addressed in the present study.

2. Materials and Methods

2.1. Fish stock and rearing conditions: Experimental fish were of Loch Lochy stock, maintained at the Buckieburn Freshwater Research Facility, Scotland (56°N) under ambient water temperatures (Fig. 1). From first feeding on 29th March, 800 fish were placed into each of eleven 2m square tanks which were constantly illuminated (LL) by 500 watt halogen lights providing 3800 lux at the water surface and 1200 lux at the tank floor (0.3m) (photometric sensor, Skye Instruments Ltd., UK). Flow rates were 1 $l.s^{-1}$ and oxygen levels remained above 8 $mg.l^{-1}$. Feed was supplied at the manufacturer's recommended rate (Trouw Aquaculture) and was distributed evenly throughout the light phase.

On 18th May four experimental treatments were created (Fig. 1) within the 11 tanks as follows:

- May winter photoperiod - Triplicate tanks with an eight week winter photoperiod (LD 10:14) starting on 18th May. LL thereafter.
- August winter photoperiod - Triplicate tanks with an eight week winter photoperiod (LD 10:14) starting on 9th August. LL thereafter.
- September winter photoperiod - Triplicate tanks with an eight week winter photoperiod (LD 10:14) starting on 22nd September. LL thereafter.
- Constant light (LL) - Duplicate tanks exposed to LL throughout.

On 25th July, 100 individuals from each tank were PIT tagged (AVID tags, Norco, Ca., USA) and the adipose fin removed. Size at tagging was approximately 4g and mortality <5%. Individuals from the May photoperiod group were not tagged as they were too small.

2.2. Sampling regime: From 25th July individual fork lengths (±1mm) and weights (±0.1g) were recorded, under anaesthesia, twice monthly in all groups to ensure the identification of first maturation and the timing of growth divergences between cohorts. Condition factor was calculated as: weight (g).fork length (cm)$^{-3}$.100. At each sampling all non-PIT tagged fish were assessed for maturity i.e. the presence of running milt.

At two week intervals, from 4th October, 15 randomly selected individuals per treatment were exposed to a 96h seawater (37.5 ppt) tolerance test (Saunders et al, 1985) and mortalities recorded.

On 4th January 2001, 100 non-tagged individuals per treatment group were killed and dissected to quantify internal signs of maturation i.e. enlarged gonadal tissue. The tagged fish from all groups were then randomly divided into two 2m^2 tanks and maintained on LL until 7th February 2001 at which point they were measured for fork length and weight; sacrificed and maturity assessed by internal examination.

At the conclusion of the experiment fish were classified into five cohorts based on morphology (Birt and Green, 1986) as follows:

1. Smolts: Fully silvered fish with no parr marks and black margins on the fins.
2. “Large” smolts: Fully silvered fish with no parr marks with black margins on the fins. These fish were significantly larger than the smolts described above (i.e. >100g).
3. “Silvered” parr: Fish that were partially silvered with parr marks that were obscured but still visible.
4. Parr: Fish showing no signs of silvering and with the presence of distinct parr marks.
5. Small parr: Fish showing no signs of silvering, with the presence of distinct parr marks but that were significantly smaller than the parr described above (i.e. <10g).

2.3. Statistical analysis: Data were analysed using Minitab v13.1. Changes in weight and condition factor were compared using a General Linear Model. Residual plots were used to confirm normality and homogeneity of variance. A significance level of 5% was applied to statistical tests (Zar, 1999).

3. Results

3.1. Maturation: The 4 photoperiod regimes had clear effects on maturation (Fig. 2). Maturing fish were first observed in early October and continued to be identified until the conclusion of the experiment in all groups. In the May photoperiod group the percentage of mature males rose sharply between early and mid-November with levels reaching approximately 20% of all fish by December and remaining above 20% until February. Under constant light the percentage of maturing fish increased to 8% during early November and remained unchanged through to February. August and September treatments resulted in maturity levels of approximately 3% from October onwards.

3.2. Growth: Under LL fish destined to become small parr were significantly smaller than all other cohorts in August (Fig. 3a). Smolts were significantly larger than mature parr by mid-September ($p<0.05$) with immature parr differing from smolts by early October. However, it was not until mid-October that the parr cohort showed significant differences between immature and mature fish ($p<0.05$).

In the August photoperiod group all cohorts except small parr remained of a similar size until 16th November (Fig. 3b). Fish destined to mature as parr were significantly larger than small parr by July ($p<0.05$), whereas remaining cohorts did not differ significantly until August. In mid-November smolts were significantly larger than precocious parr ($p<0.05$). Immature parr only differed significantly from the smolts and precocious parr from late November ($p<0.05$).

All the cohorts except small parr in the groups under the September photoperiod remained of similar size until mid-December (Fig. 3c). Immature parr diverged from small parr in early August with smolts larger by mid-August and mature parr heavier by early September ($p<0.05$). Smolts and parr had similar weights until mid-December when smolts were heavier than mature parr. In early January the weights of all groups were statistically different ($p<0.05$). However, by the end of the experiment, in early February, the weights of immature parr and smolts were similar ($p>0.05$).

In the May photoperiod group only the growth of immature or mature fish could be studied (Fig. 3d). However, no significant differences in weight were observed between immature and mature fish ($p>0.05$).

Under LL both immature and mature parr showed initial increases in condition factor (Fig. 4a) with immature, mature and small parr showing an overall decline in CF, from approximately 1.25 to 1.15, by January ($p<0.05$). However, with the exception of immature and mature parr, which were significantly different from late September onwards, no consistent differences occurred between cohorts throughout the experiment.

In the August photoperiod, CF initially rose in smolt, immature parr and small parr groups (Fig. 4b) with all cohorts showing an overall decline in CF by January ($p<0.05$). Smolts also showed a significant decline during October although no consistent differences were observed between cohorts.

Smolts, immature parr and small parr all showed initial increases in CF under the September photoperiod (Fig. 4c) with only the condition factor of immature parr significantly decreasing by January ($p<0.05$). Again no consistent differences were observed between cohort groups.

A May photoperiod resulted in an initial rise in the CF of immature fish (Fig. 4d) with an overall decrease by January ($p<0.05$). However, the CF of mature fish did not decline or differ significantly with the CF of immature parr throughout the experiment ($p>0.05$).

Between treatment differences in CF only occurred in immature parr and smolt cohorts. For immature parr the CF of LL and August photoperiod groups remained similar, with the CF of both groups higher than that of the immature parr from the

September photoperiod. These differences remained from July until late September for the LL group and throughout the experiment for the August photoperiod fish. The CF of smolts only differed between August and September photoperiod groups with August photoperiod smolts having a higher CF from November until the end of the experiment ($p<0.05$).

3.3. Seawater Tolerance: Survival rates following seawater exposure showed variable results in the LL group as well as in the May and September photoperiod groups throughout the experiment (Fig. 5). However, fish exposed to an August winter photoperiod showed increases in survival from 4th October, reaching 100% during late November, before declining slightly in early January.

3.4. Cohort Structure: Photoperiod manipulation resulted in distinct differences in population structure (Table 1). LL resulted in 92% of the population remaining as parr, including 10% that matured. The May photoperiod treatment caused 49% of the population to develop as parr. The remainder of the population included fish from all cohort classes and it was only in this group where the presence of “large” smolts was observed. Every cohort in this group exhibited mature individuals. A winter photoperiod in August provided the highest percentage of immature smolts (19%), silvered parr (30%) and small parr (21%). Again, all cohort classes included maturing fish. A winter photoperiod in September resulted in the majority of fish remaining as parr (59%) with 28% appearing as silvered parr. Small parr were also observed (13%) but the incidence of maturing individuals was restricted to parr (9%) and small parr (1%).

4. Discussion

Varying the time of exposure of Atlantic salmon parr to 8 week periods of short days resulted in significant effects on both smoltification and maturation with early exposure resulting in the highest levels of maturation.

The timing of maturation in salmonids is said to be most stimulated by an initial period of long days followed by a period of short days (Bromage et al., 1984; Elliott et al., 1984; Takashima and Yamada, 1984). In the present work, high levels of maturation were observed in the May photoperiod group confirming the importance of a reduction to short days in the control of maturation in parr development. However, the absence of high levels of maturing fish in the two groups exposed to winter photoperiods in August and September, indicates that a period of short days is not necessarily required for maturation to be completed. Eriksson and Lundqvist (1980) noted that a sudden change from long to short days did not necessarily induce maturation in Baltic salmon parr. However, Berg et al. (1994), reported similar results to the present study, with a 7 week period of LD14:10 resulting in high levels of maturation in Atlantic salmon parr. The early period of reduced daylength may initiate reproductive development or phase shift the reproductive cycle (Duston and Bromage, 1986). It has been shown that photoperiod manipulation (Porter et al., 1999; Taranger et al., 1999) and feeding restriction (Rowe and Thorpe, 1990a; Berglund, 1995; Hopkins and Unwin, 1997) at seasonally critical times, can suppress maturation with springtime being suggested as the critical period (Rowe and Thorpe, 1990a; Berglund, 1995; Taranger et al., 1999). However, this implies that the developmental choice to mature has already been taken and it may be that it is not the timing that is as important as the developmental stage of the fish. Furthermore, it is well documented that maturing fish are initially among the fastest growing individuals within a population (Saunders et al., 1982; Dalley et al., 1983; Rowe and Thorpe 1990b; Berglund, 1992) and it seems from the present work that the period, shortly after first feeding, may be an important one in the decision to mature.

Under LL, maturation still occurred indicating that maturation is controlled by an endogenous rhythm, entrained by photoperiod, as suggested by Eriksson and Lundqvist (1982), Bromage et al. (1984), Elliott et al. (1984) and Duston and Bromage (1986). However, the timing of maturation between treatment groups was similar, therefore a phase shift of the rhythm had not occurred.

Previously, Thorpe and Morgan (1980) and Thorpe (1986) suggested that smoltification and maturation were mutually exclusive and smolting occurred as a consequence of failing to mature (Thorpe, 1994b, Thorpe and Metcalfe, 1998). The results presented here, as well as those of Bagliniere and Maisse (1985), Whalen and

Parrish (1999) and Utrilla and Lobón-Cerviá (1999) show that these processes are not exclusive. Salmon need to attain a threshold size before they can either mature (Berglund, 1992) or smolt (Elson, 1957; Skilbrei, 1988) and Saunders et al. (1982) suggested that the maturation threshold is lower than that for smoltification. Furthermore, the reduced growth rate of maturing fish (Rowe and Thorpe, 1990b) may preclude such individuals from smolting. In the current study the May and August photoperiods were proceeded by long periods of constant light and under such conditions of good growth it has been suggested that certain fish may first attain a suitable size to mature, and then continue to grow such that smoltification is also possible (Villareal et al., 1988; Solbakken et al., 1994). Furthermore temperature is an important factor in growth (Herbinger and Friars, 1992; Duston and Saunders, 1997) and as such can be a determinant in the decision to both mature (Adams and Thorpe, 1989; Solbakken et al, 1994) and smolt (Solbakken et al, 1994; Duston and Saunders, 1997). In the May photoperiod group, the period of increased ambient temperature, prior to the application of the winter photoperiod, as well as elevated temperatures during the applied winter and spring/summer may have enhanced the number of fish choosing to mature. For August photoperiod fish it is possible that the decline in temperature following the return to LL may have resulted in fish opting to undertake smoltification as opposed to maturation. For September photoperiod fish it seems that the winter photoperiod and subsequent LL occurred at temperatures which were too low to greatly enhance the numbers of either mature or smolting fish.

Finally, the feeding regime applied to treatment groups may have influenced the decisions to both mature and smolt. All groups were fed at the same rate throughout the respective light phases of the specified photoperiods. Higgins and Talbot (1985) noted that photoperiod was influential in regulating food intake, and indeed in the current study fish exposed to winter photoperiod regimes were fed over a shorter period of time (although total feed rates were not reduced). During artificial winter photoperiods growth is always suppressed and therefore it is unlikely that the feeding regime curtailed growth rates.

In conclusion the current study shows that photoperiod has a major influence on the incidence of precocious maturation as well as smoltification in Atlantic salmon parr.

It also showed that some individuals were able to mature and then undergo smoltification showing that the two processes are not mutually exclusive. A period of short days, early in development, increased the percentage of the population which showed early maturation. These results suggest that under current farming conditions the use of increasingly early winter photoperiods, to further advance smoltification, may result in increased incidences of precocious maturation.

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Fig. 1. Ambient water temperature relative to the 4 experimental photoperiod regimes. a) constant illumination (LL), b) May photoperiod, c) August photoperiod, d) September photoperiod.

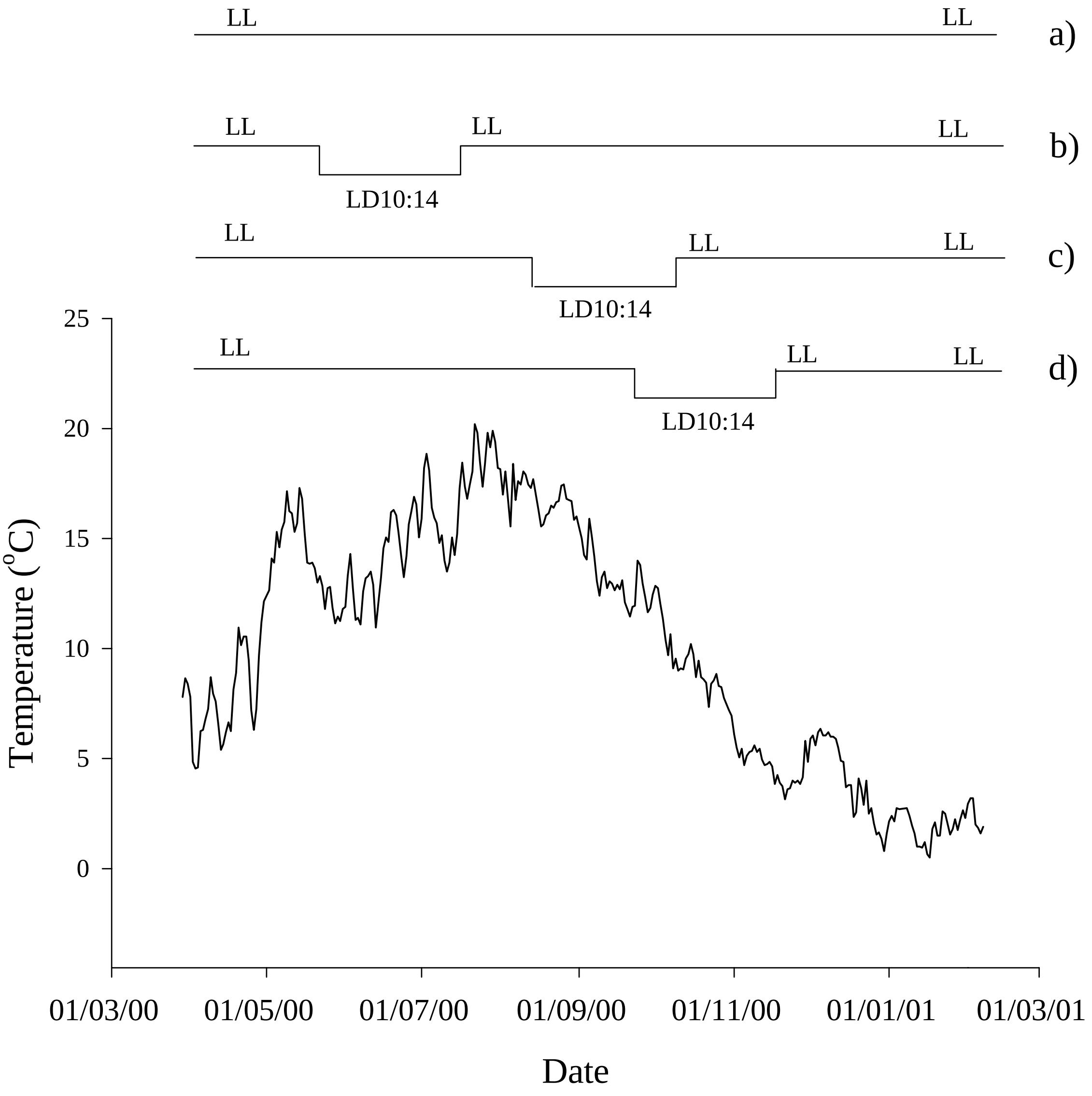
Fig. 2. Cumulative percentages of precocious males in the four experimental treatments. Values were for all non-tagged individuals within the population with maturity based on the presence of running milt.

Fig. 3. Changes in weight of the 4 cohorts of individually PIT tagged fish following exposure to constant illumination (LL) (a), August photoperiod (b), September photoperiod (c) and May photoperiod (d) regimes (mean ± S.E.M., n=100 for constant illumination, August photoperiod and September photoperiod groups, n=30 for May photoperiod fish). For the May photoperiod group only mature and immature fish are shown due to the absence of tagging in that group. Values with different letter labels are significantly different ($p<0.05$). Lettering has been stacked in the same order as the graph lines.

Fig. 4. Changes in condition factor of the 4 cohorts of individually PIT tagged fish following exposure to constant illumination (LL) (a), August photoperiod (b), September photoperiod (c) and May photoperiod (d) regimes (mean ± S.E.M., n=100 for constant illumination, August photoperiod and September photoperiod groups, n=30 for May photoperiod fish). For the May photoperiod group only mature and immature fish are shown due to the absence of tagging in that group. Values with different letter labels are significantly different ($p<0.05$). Lettering has been stacked in the same order as the graph lines.

Fig. 5. Percentage survival following a 96h seawater (37.5ppt) tolerance test for fish exposed to the 4 photoperiod regimes.

Fig. 1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LD10:14
LL
LL
LL
c)
LD10:14
LL
LL
LL
d)
LD10:14
25
20
15
10
5
0
Temperature (^{o}C)
01/03/00
01/05/00
01/07/00
01/09/00
01/11/00
01/01/01
01/03/01
Date

Fig. 2

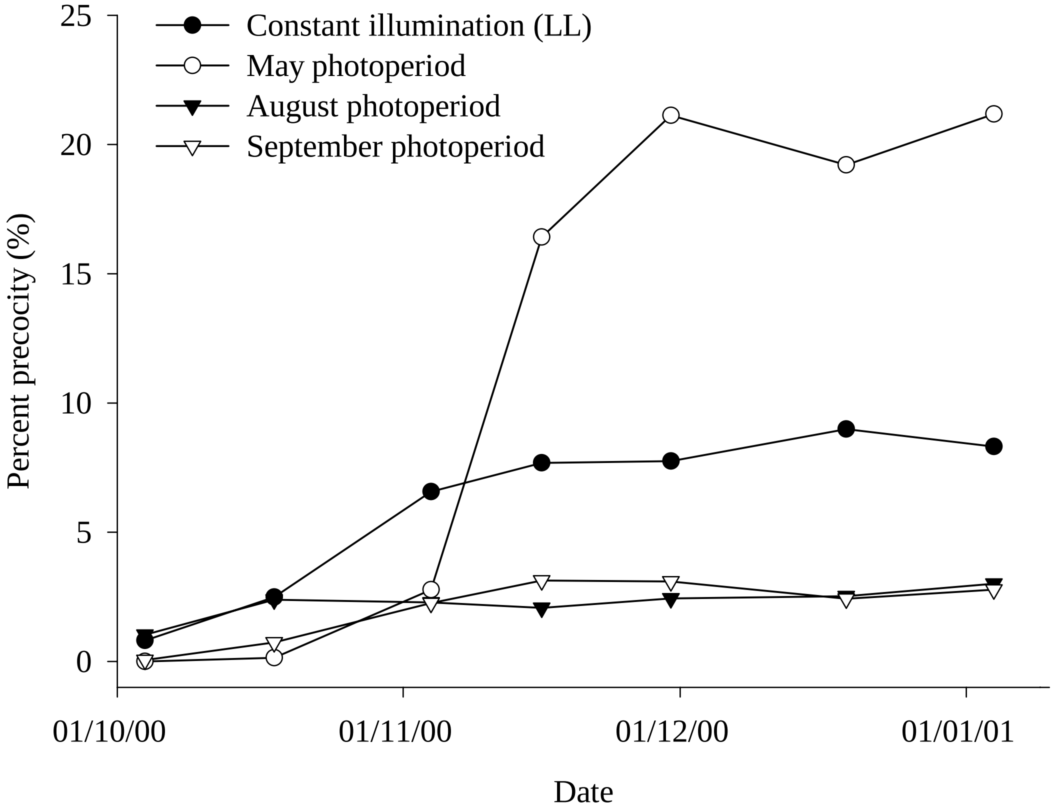
Constant illumination (LL)
May photoperiod
August photoperiod
September photoperiod
Percent precocity (%)
0
5
10
15
20
25
01/10/00
01/11/00
01/12/00
01/01/01
Date

Fig. 3

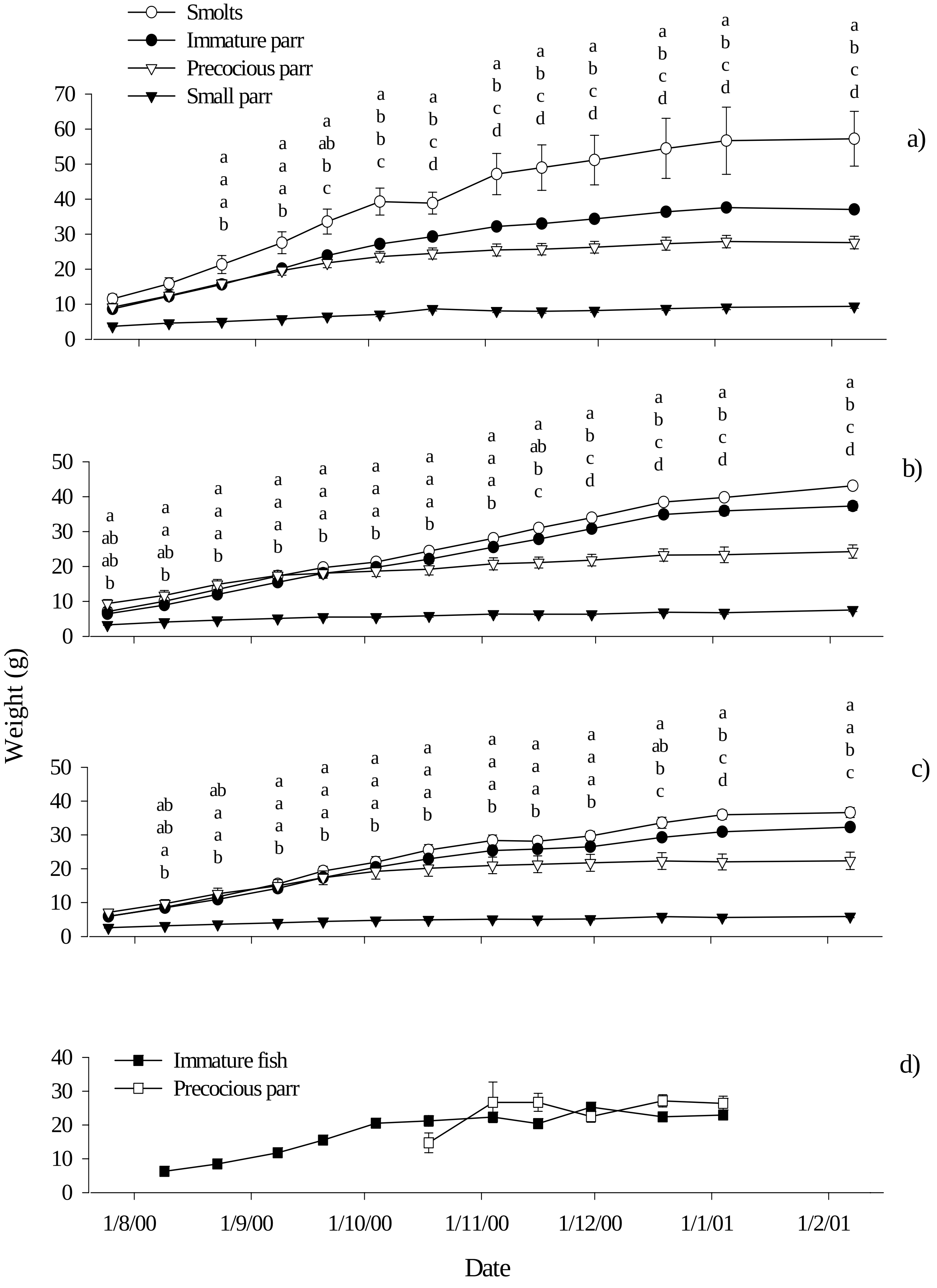
Smolts
Immature parr
Precocious parr
Small parr
a)
b)
c)
d)
70
60
50
40
30
20
10
0
a a a b
a a a b
a ab b c
a b b c
a b c d
a b c d
a b c d
a b c d
a b c d
a b c d
a b c d
a ab ab b
a a ab b
a a a b
a a a b
a a a b
a a a b
a a a b
a a a b
a ab b c
a b c d
a b c d
a b c d
a b c d
ab ab a b
ab a a b
a a a b
a a a b
a a a b
a a a b
a a a b
a a a b
a a a b
a ab b c
a b c d
a a b c
Immature fish
Precocious parr
Weight (g)
1/8/00
1/9/00
1/10/00
1/11/00
1/12/00
1/1/01
1/2/01
Date

Fig. 4

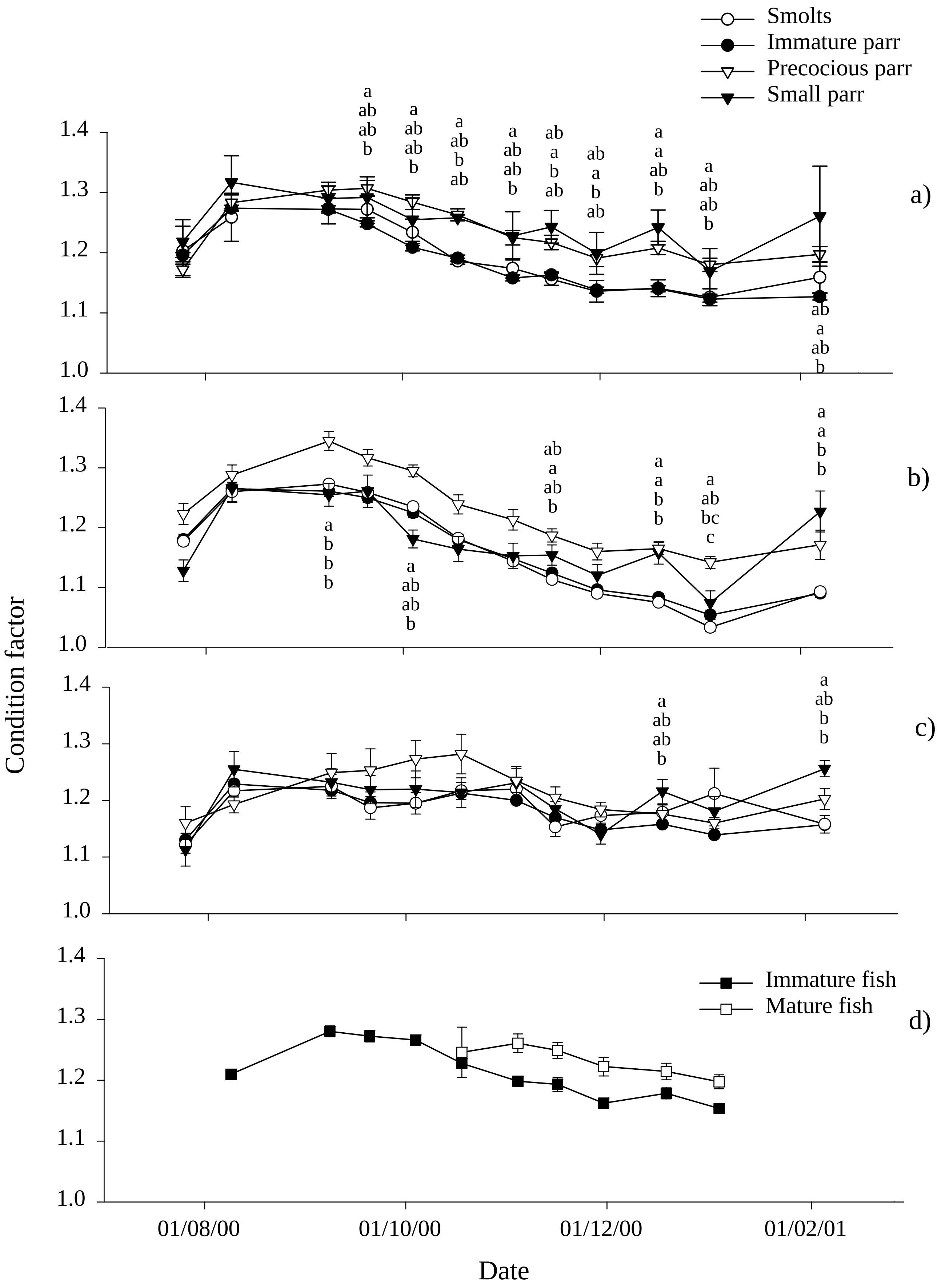
Smolts
Immature parr
Precocious parr
Small parr
a)
b)
c)
d)
Immature fish
Mature fish
Condition factor
1.0
1.1
1.2
1.3
1.4
a ab ab b
a ab ab b
a ab b ab
a ab ab b
ab a b ab
ab a b ab
a a ab b
a ab ab b
ab a ab b
a b b b
a ab ab b
ab a ab b
a a b b
a ab bc c
a a b b
a ab ab b
a ab b b
01/08/00
01/10/00
01/12/00
01/02/01
Date

Fig. 5

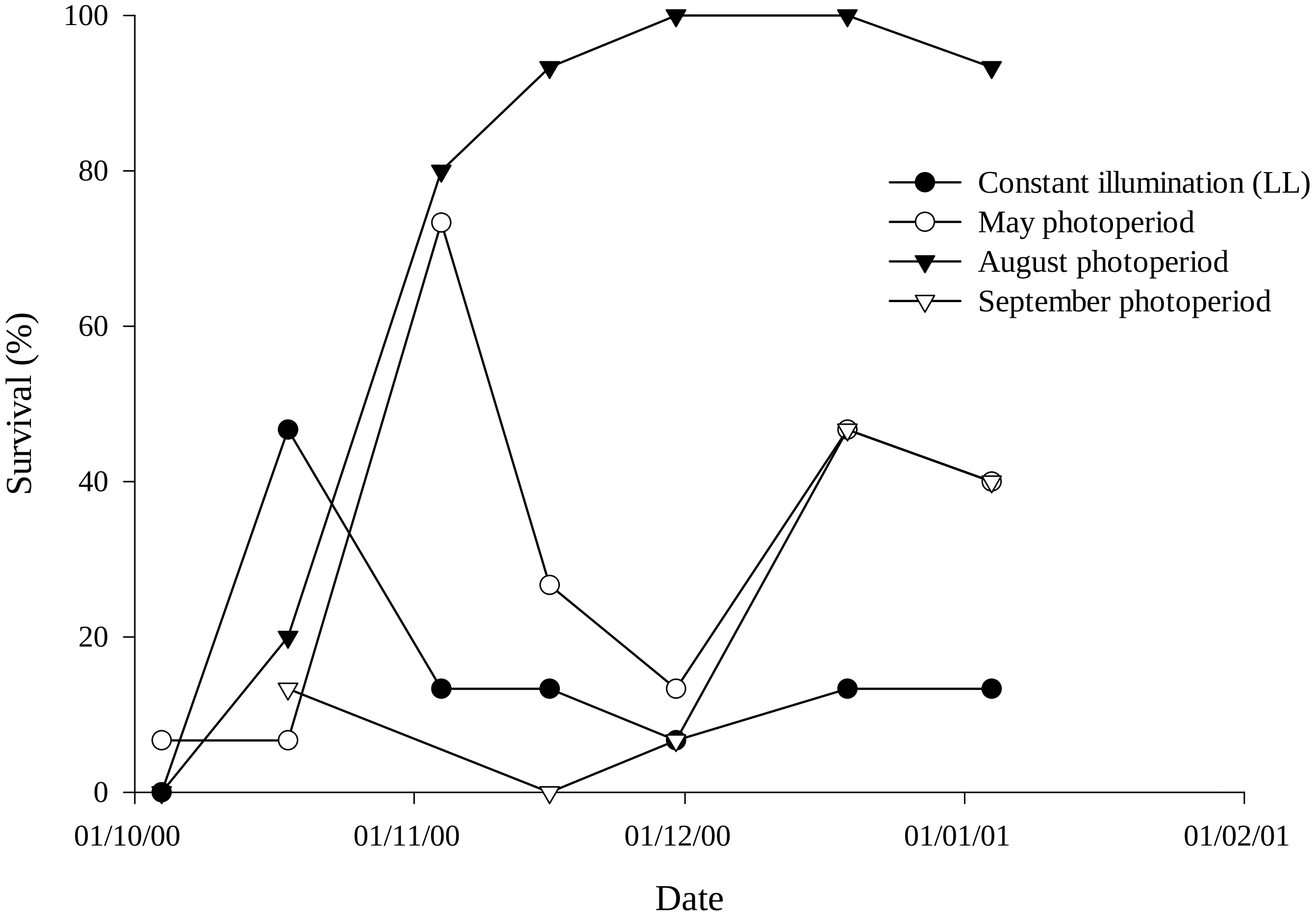
100
80
60
40
20
0
Survival (%)
01/10/00
01/11/00
01/12/00
01/01/01
01/02/01
Date
Constant illumination (LL)
May photoperiod
August photoperiod
September photoperiod

Table 1. The effects of varying the timing of exposure to an 8 week winter photoperiod on the cohort structure (based on external appearance) and internal signs of maturation of non-tagged individuals within the population at the conclusion of the experiment (4th January 2001). Refer to Materials and Methods for details of cohort nomenclature. Imm denotes immature fish, Mat denotes mature fish.

	Constant illumination		May photoperiod		August photoperiod		September photoperiod	
	Imm	Mat	Imm	Mat	Imm	Mat	Imm	Mat
"Large" smolts	-	-	14%	4%	-	-	-	-
Smolts	-	-	1%	1%	19%	1%	-	-
Silvered parr	6%	-	10%	3%	30%	7%	28%	-
Parr	82%	10%	38%	11%	13%	7%	50%	9%
Small parr	2%	-	13%	5%	21%	2%	12%	1%