A decrease in photoperiod shortly after first feeding influences the development of Atlantic salmon (Salmo salar).

Berrill, I. K. [a] *, Smart, A.[b], Porter, M. J. R. [c] and Bromage, N. R. [a]

[a] Institute of Aquaculture, University of Stirling, Scotland, FK9 4LA.

[b] PO Box 106, Melrose, South Australia, 5483.

[c] School of Aquaculture, University of Tasmania, Launceston, 7250, Tasmania, Australia.

[*] Corresponding author. Current address: School of Ocean Sciences, University of Wales, Bangor, Menai Bridge, Anglesey, LL59 5AB. UK. Tel.: +44 1248 351151 Fax: +44 1248 716367. E-mail: i.k.berrill@bangor.ac.uk

Abstract

Four groups of Atlantic salmon fry (n=2000) were exposed to continuous light (LD24:0) from first feeding on 18th April 2001, after which they were exposed to either an 8 or 12 week period of short days (LD10:14) starting on either the 21st May or the 18th June. Each group was then returned to LD24:0 until the conclusion of the experiment the following March. In August 200 fish per treatment were individually PIT tagged. All groups were maintained under an ambient temperature regime.

The highest levels of sexual maturation in 0+ male parr were recorded in the 12 week/May group (>11% of the entire male and female population), with the lowest levels (<1%) in the 12 week/June treatment and intermediate levels (>6%) in the 8 week/May and 8 week/June groups ($P<0.05$). Between mid August and late October mature parr were heavier than their immature counterparts, but subsequently both cohorts maintained similar sizes. Fish showing signs of silvering were found from mid October onwards. However it was only in the 12 week/June group that silvered fish had a significantly reduced condition factor and an increased gill Na^+, K^+-ATPase activity, indicative of smoltification. At the conclusion of the experiment, fish showing signs of silvering were most prevalent (30%) in the 12 week/June group.

It is concluded that the initiation of maturation can be influenced by an 8 or 12 week period of short days (LD10:14) applied from mid May or mid June in the first growing season. The duration and timing of a stimulatory short day photoperiod during early development may also influence whether a fish undergoes smoltification in the coming year or whether it delays the parr-smolt transformation for at least a further year.

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

1. Introduction

In recent years efforts have been made to understand variations in the life history strategies of juvenile Atlantic salmon. A prominent aspect of juvenile salmonid development when reared under a natural photoperiod regime is the emergence of a bimodal population structure during late summer in the first growing season (Thorpe, 1977; Kristinsson et al., 1985; Skilbrei, 1988), with this division determining which fish will smolt in the following spring and which will remain in fresh water for a least a further year (Thorpe, 1977; Kristinsson et al., 1985). Increasingly, accelerated production regimes are used stabilize seasonal fluctuations in the production of smolts and market sized fish. Photoperiod manipulation in particular can be used to influence the numbers of smolts and the yearly timing of seawater transfer. Similar to the influences received in the wild, a short day, winter photoperiod can be used to initiate smoltification, with the parr-smolt transformation then completed during a long day spring regime (Duston and Saunders, 1992; Sigholt et al., 1995; Duncan and Bromage, 1998). However, in using accelerated rearing regimes the incidence of sexual maturation can also be affected. Parr maturation is usually only found in male salmon, due to the lower nutritional requirements for male gonadal development (Adams and Thorpe, 1989), and although mature parr have been found to undergo smoltification (Saunders et al., 1994; Duston and Saunders, 1997), maturation can inhibit the parr-smolt transformation to some degree (Thorpe and Morgan, 1980), with increased androgen levels during maturation thought to play a role in this inhibitory process (Aida et al., 1984; Miwa and Inui, 1986). Mature parr are therefore poorly adapted to seawater (Saunders et al., 1994) and they are typically removed from commercial populations as soon as they are identified.

Maturation is influenced by a photoperiodically entrained endogenous rhythm(s) (Bromage et al., 1984; Duston and Bromage, 1986) which can be advanced by a long- and then short day photoperiod regime (Bromage et al., 1984). As a result of these photoperiodic cues complex interactions can occur between the initiation and completion of both maturation and smoltification. However, further to these influences it is believed that a size and/or nutritional threshold has to be surpassed before smoltification (Elson, 1957; Kristinsson et al., 1985) and maturation (Thorpe and Morgan, 1980; Saunders et al., 1982) can occur. It is also likely that maturation in particular can be influenced by such thresholds during specific times in development. Metcalfe (1998) and Thorpe et al. (1998) suggested that maturation could be initiated in November, although it could be "switched off" during a second sensitive period in spring. Furthermore, Thorpe (1994) has suggested that the initiation of maturation could be influenced prior to first feeding. Similarly, Berrill et al. (2003) found that an 8 week period of short days (LD10:14) applied in May, shortly after first feeding in March, increased maturation rates compared to similar regimes applied later in the summer, highlighting a specific period of sensitivity in early development.

Clearly, the interactions between winter photoperiod and life history strategy are poorly understood, especially with regards to early development. Consequently, the current study leads on from that of Berrill et al. (2003) and aims to investigate the importance of the timing and duration of short day photoperiod regimes during a proposed sensitive period in early development. In order to achieve this 8 and 12 week periods of short days were applied at two times from shortly after first feeding.

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 (Lat. 56°N) under ambient water temperatures (monthly averages ranged from 14.9^{o}C in August 2001 to 3.1^{o}C in December 2001). Flow rates were 1 l.s^{-1} and oxygen levels were >8 mg.l^{-1}. Feed was supplied at the manufacturer's recommended rate (Trouw Aquaculture; UK), throughout the light phase of the photoperiod.

2.2. Experimental regimes: From first feeding on 18th April 2001, 1000 fish were placed into each of eight 2m square tanks and exposed to LD24:0. On both 21st May and 18th June, two duplicate groups were exposed to either an 8 or 12 week winter photoperiod (LD10:14) after which they were returned to LD24:0 until the conclusion of the experiment in March 2002 (Table 1). This created four treatments termed: the 8 week/May, 12 week/May, 8 week/June and 12 week/June treatments respectively. The timing of the photoperiods was determined in order to compliment the study of Berrill et al. (2003); in the current experiment the May treatments replicated the yearly timing of the May photoperiod group of Berrill et al. (2003) regardless of age from first feeding. Then, due to a difference in the time of first feeding between the two experiments, the fish from the June photoperiods of the current experiment were of a similar chronological age as the May photoperiod fish from Berrill et al. (2003).

On 13th August, 100 fish per tank were P.I.T. tagged (AVID tags, Norco; Ca., USA), with the adipose fin removed for identification. Size at tagging was 4.4±0.1g (mean±S.E.M.) and mortality <1%. In October, due to hatchery constraints, the

replicates from each treatment were pooled into one of four, 4m diameter circular tanks. Prior to this there were no significant differences in fish size between replicates ($P>0.05$). In late January a stand-pipe accident resulted in significant losses from the 12 week/May group and at this point the treatment was terminated.

2.2. Sampling regime: On 19th April and 17th May six batches of 100 fish were weighed (±0.1g) and the fork lengths (±1mm) of 100 fish recorded from each treatment. Then at two week intervals from 18th June until 16th July 100 individual fork length and weight measurements were made from each treatment. From August until late January, fork length and weight measurements were recorded from all tagged fish at twice monthly intervals, and then from late January onwards monthly measurements were taken. At six week intervals 60 non-tagged individuals per tank were sampled to confirm that neither length nor weight had been affected by tagging ($P>0.05$).

At each sample point all fish were examined to assess the number of mature males, with individuals recorded as mature only if milt could be expressed following slight abdominal pressure. At each sample point from mid October, when fish were first identified with signs of silvering, gill samples were taken from 20 randomly selected non-tagged fish per treatment for the assessment of Na^+, K^+-ATPase activity using the method detailed by McCormick (1993). For analytical purposes individuals sampled for Na^+, K^+-ATPase were divided into those showing signs of external silvering and those that appeared as parr. The weights (±0.1g) of the fish sampled for Na^+, K^+-ATPase activity were also recorded.

At the conclusion of the experiment in March 2002, it was clear that the population structure of the groups was complex. Consequently all tagged and 150 non-tagged fish per treatment were classified into one of four cohorts, based on morphology (Birt and Green, 1986), maturity status and size:

1. Silvered fish (0+): Large (>180mm) fish with some or complete silvering. From the data collected these fish were viewed as 0+ smolts.
2. Immature parr (1+): Fish showing no signs of silvering and with the presence of distinct parr marks. These fish were significantly smaller (<180mm) than the silvered fish. It was believed that these fish would smolt at age 1+.
3. Mature parr (1+): These fish were similar in size and appearance to immature parr but with the exception that they were mature. i.e. they did not typically display the morphology often recorded in mature male parr (reduced size, dark parr marks).
4. Small parr (2+): Small fish (<110mm) showing no signs of silvering, with the presence of distinct parr marks. It was believed that these fish would smolt at age 2+.

2.3. Statistical analysis: Condition factor was calculated as: weight (g).fork length $(cm)^{-3}$.100. Data were analysed using Minitab v14. Changes in weight, condition factor and Na^+, K^+-ATPase activity were compared using a General Linear Model (GLM). To satisfy the assumptions for the GLM, natural log transformations were used for the weight data. Where data from P.I.T. tagged fish were analysed, a nested design was used to account for the repeated measures sampling. Residual plots were used to confirm normality and homogeneity of variance. To analyse the final mean weights of each population, non-parametric Kruskal-Wallis tests were used, followed by Dunn's multiple comparison test. To analyse the percentage maturation and

population structure data, 95% confidence intervals were calculated (Fowler and Cohen, 1987) and compared such that if the confidence intervals did not over lap the proportions were considered significantly different ($P<0.05$). A significance level of 5% was applied to the statistical tests (Zar, 1999).

3. Results

3.1. Final weight and population structure: At the conclusion of the experiment in March 2002, the mean weights (± S.E.) of the fish within each treatment (regardless of population structure) were 29.8±1.0g, 23.6±1.6g, 34.5±2.1g and 31.9±2.7g for the 8 week/May, 12 week/May, 8 week/June and 12 week/June groups respectively. The 8 week/June fish were significantly larger than both 12 week groups ($P<0.01$), with the 8 week/May fish larger than the 12 week/May group and smaller than the 12 week/June fish ($P<0.01$).

At the conclusion of the experiment, similar population structures were found in the 8 week/May, 12 week/May and 8 week/June groups (Table 2), with immature parr (68%, 62% and 65% respectively) the most prevalent cohort ($P<0.05$), low numbers of silvered fish (4%, 4% and 8% respectively) and a similar ($P>0.05$), intermediate incidence of mature and small parr. In the 12 week/June group the incidence of silvered fish and small parr was higher than in the other treatments (30% and 31% respectively) with lower numbers of immature (35%) and mature parr (4%) ($P<0.05$).

3.2. Growth: In mid June, prior to P.I.T. tagging, fish from both May treatments were smaller than the 8 week/June fish, which were still being exposed to LD24:0 (Fig. 1). At this time, fish from the 8 week/May group were also smaller than the 12

week/June fish ($P<0.05$). From early July, when all treatments were exposed to LD10:14, both May photoperiod groups were smaller than the June fish ($P<0.05$) although the 8 week/May fish were larger than the 12 week/May fish. By mid July, fish from the May treatments had become similar in size, remaining smaller than the June fish ($P<0.05$).

After P.I.T. tagging on 13th August, all cohorts increased in weight over the experimental period ($P<0.001$) although differences occurred in the size of fish from particular cohorts between the treatments (Fig. 2). Fish classified as "silvered fish" at the conclusion of the experiment were smallest in the 8 week/May group from late November onwards, with those from the 8 week/June treatment larger than the 12 week/May and 12 week/June fish until mid November and the conclusion of the experiment respectively ($P<0.05$). Immature parr were smallest in the 12 week/June group ($P<0.05$), with those from the 12 week/May treatment smaller than both 8 week groups until late October ($P<0.05$). For mature parr no clear trends emerged, whereas small parr from the 8 week/May group were the smallest from late October ($P<0.05$).

Differences were also found when the four cohorts were compared within each treatment (Fig. 3). From early August in the 8 week/May, 8 week/June and 12 week/June groups, silvered fish were the heaviest individuals, with small parr the smallest and immature parr intermediate in weight ($P<0.001$). In the 12 week/May group, silvered fish were heavier than immature parr from late October ($P<0.001$), with small parr the smallest fish from mid August ($P<0.001$).

In the 8 and 12 week/May groups, mature parr were heavier than immature parr between September and October ($P<0.05$), with those from the 8 week/June treatment heavier from mid August until late October ($P<0.05$). At all other times, and throughout the 12 week/June treatment, mature and immature parr maintained similar weights ($P>0.05$).

For condition factor, the most significant temporal change occurred in the silvered fish from the 12 week/June group (Fig. 4), where condition declined to a minimum in late November before rising to the conclusion of the experiment ($P<0.001$). In the 8 week/May, 8 week/June and 12 week/June treatments the condition of silvered fish, immature parr and small parr declined over the course of the experiment, with that of the 8 week/June mature parr also decreasing ($P<0.01$). In the 12 week/May group only the condition of the immature parr decreased during the experiment ($P<0.01$).

In the 8 week/May, 12 week/May and 8 week/June groups, mature parr maintained the highest condition. In the 8 week/May group, mature parr had a higher condition than silvered fish and small parr from early October until early January and mid February respectively ($P<0.05$), with the condition of immature parr lower from mid August until early January ($P<0.01$). In the 12 week/May group, mature parr had a higher condition than immature parr from mid October until late November ($P<0.01$). Mature parr in the 8 week/June group had a higher condition than silvered fish from late October until mid February, with that of immature parr lower in October ($P<0.05$).

In the 12 week/June group, the condition of silvered fish was lower than that of the immature parr and small parr from October until mid March ($P<0.01$), and lower than the mature parr from October to mid February ($P<0.05$).

3.3. Maturation: Mature fish were first identified in the 8 week/May and 8 week/June groups in late October (Fig. 5) and during November and December the incidence of maturation increased in all treatments. The highest levels of maturity were found in the 12 week/May group ($P<0.05$), rising to a peak (>11% of the entire male and female population) in early January. From late November levels of maturity in the 8 week/May and 8 week/June treatments remained similar ($P>0.05$) with peaks of approximately 6% in mid December and early January respectively. The 12 week/June group had the lowest incidence of maturity ($P<0.05$), with levels never exceeding 1%.

3.4. Na^+, K^+-ATPase: In the 12 week/June group, silvered fish had higher gill ATPase activities than non silvered fish until mid December ($P<0.05$) (Fig. 6), although no differences were found within the other treatments. However, throughout the experiment ATPase activities did not exceed 6μmol ADP hydrolysed^{-1}. mg protein^{-1}. h^{-1} and they did not increase over the course of the experiment. In the 12 week/June group silvered fish weighed more than non silvered fish ($P<0.001$), although no clear trends could be found in the other treatments.

4. Discussion

The timing and duration of a period of short days, applied during early development, influenced the growth and development of juvenile Atlantic salmon. Previously Berg

et al. (1994) and Berrill et al. (2003) have shown that a period of short days, applied shortly after first feeding, influences the initiation of maturation and the current experiment provides further support. The incidence of maturation was highest in the 12 week/May group and lowest in the 12 week/June treatment. This implies that the initiation of maturation occurs near to first feeding and that the proposed period when maturation can be influenced (Saunders et al., 1982; Thorpe, 1994) may be fairly rigid in duration, such that slightly later in the year (i.e. June) short days will not be as influential. Furthermore, as intermediate levels of maturation were found in the 8 week groups, it seems that during this period, 12 weeks of short days will influence maturation to a greater level than 8 weeks.

In the current study fish that were destined to mature were larger than immature parr until October. However, after this period immature and mature fish maintained similar weights, with the 12 week/June fish maintaining similar weights throughout the experiment. Previously Naevdal (1983) reported a similar finding although the majority of evidence suggests a divergence in the size of mature and immature fish (Dalley et al., 1983; Rowe and Thorpe, 1990; Berglund, 1995) in particular as gonadal development ensues (Berglund, 1992), which results in mature fish being smaller than immature individuals at maturation (Dalley et al., 1983; Saunders et al., 1982). Clearly, the short day regimes experienced in the current experiment influenced the growth of mature and/or immature fish although the mechanisms by which this has occurred are not known. However, it is important to note that as well as the short day regimes, an interaction between the subsequent extended period of continuous light may have been influential in the observed growth profiles, particularly during the warm summer months, as both light and increased

temperatures can provide good conditions for growth (Solbakken et al., 1994; Sigholt et al., 1995; Handeland and Stefansson, 2001).

The gill Na^+, K^+-ATPase activities of silvered fish and the incidence of such individuals at the conclusion of the experiment were poor in comparison to previous studies (c.f. Duncan et al., 1998; Handeland and Stefansson, 2001), with only the 12 week/June treatment resulting in fish that showed signs of undergoing the parr-smolt transformation. It is well documented that smoltification is dependant on the attainment of a specific size threshold (Elson, 1957; Skilbrei, 1988), and it is thought that this threshold must be achieved either before (Kristinsson et al., 1985; Skilbrei, 1991) or during (Duston and Saunders, 1997) winter. It is therefore likely that because the 12 week/June photoperiod was applied later in the year, with an extended period of short days, this was the only group where high numbers of fish achieved the threshold for smoltification at the appropriate time. However, it is also important to note that for the silvered fish in the 12 week/June group, gill Na^+, K^+-ATPase activity was only elevated until mid December. Therefore although silvered fish were recorded at the end of the experiment in March, it is likely that these fish had passed through the window where smoltification was possible and could not be considered as true smolts at that time.

It has previously been suggested that approximately 8 weeks of short days are sufficient to initiate smoltification (Sigholt et al. 1995; Duncan and Bromage, 1998; Duncan et al. 1998) although Duston and Saunders (1995) quote unpublished data indicating that 3 months of short days in June are better at stimulating smoltification than 2 months. In the current experiment the 12 week/June group produced more

silvered fish than the 8 week/June group and therefore it is likely that if growth is limited prior to winter, a longer period of short days may result in a greater incidence of smoltification. This also suggests that the size threshold for successful smoltification can be achieved during, and not solely prior to, winter (Duston and Saunders, 1997).

Prior to tagging the June photoperiod fish rapidly became larger than those that were exposed short days in May. It is well documented that increases in daylength enhance growth (Solbakken et al., 1994; Handeland and Stefansson, 2001) and the exposure of the June treatment fish to a longer period of continuous light prior to the application of their winter photoperiod would have resulted the observed differences in size. Following tagging individual cohorts could be investigated. However, no clear trends, such as those observed prior to tagging, could be identified between the treatments. The reasons for this absence of distinct trends are unclear, but it is possible that the short day regimes used were insufficiently different to cause any consistent differences between the groups.

Within each treatment, the cohorts of fish had either diverged in weight by the time of tagging, or did so shortly afterwards. Previously, Saunders et al. (1982) and Thorpe (1994) have suggested that the initiation of maturation occurs in early development, although it can be "switched off" during a sensitive period in spring (Metcalfe, 1998; Thorpe et al., 1998). From the findings of the current experiment, it seems that as well as maturation, the decision to smolt in the current year or in subsequent years can also be influenced during early development.

Changes in condition have been linked to maturation (Rowe and Thorpe, 1990; Duston and Saunders, 1997) and in the current experiment the condition of maturing fish was greater than immature individuals. However, the condition of mature fish was not consistently elevated above all cohorts suggesting that it may be unreliable for predicting which fish will undergo maturation (Duston and Saunders, 1997).

In conclusion, to maximise smolt production, whilst limiting parr maturation, it may be necessary to consider the use of longer periods of short days to stimulate smoltification, possibly at earlier stages in development than are currently used. Such photoperiods could allow fish that have previously been considered to small to smolt more time to achieve the threshold necessary for smoltification during the "winter" photoperiod and may also influence periods in development when maturation can be reduced. However, the current study has shown that depending on the duration and timing of such short day regimes, levels of maturation can be both increased and decreased, and consequently further research is needed before any changes to current rearing protocols can be considered.

Acknowledgements

The authors would like to thank the staff at the Buckieburn Freshwater Research Facility and Billy Robertson for advice on fish rearing and P.I.T. tagging. This work was supported by a NERC CASE award to IB and NERC ROPA and Marine Harvest Scotland grants to NB and MP.

References

Adams, C. E., Thorpe, J. E., 1989. Photoperiod and temperature effects on early development and reproductive investment in Atlantic salmon (Salmo salar L.). Aquaculture 79, 403-409.

Aida, K., Kato, T., Awaji, M., 1984. Effects of castration on the smoltification of precocious male masu salmon Oncorhynchus masou. Bull. Jap. Soc. Sci. Fish. 50, 565-571.

Berg, A., Stefansson, S.O., Hansen, T., 1994. Effect of reduced daylength on growth, sexual maturation and smoltification in Atlantic salmon (Salmo salar) underyearlings. Aquaculture 121, 294.

Berglund, I., 1992. Growth and early sexual maturation in Baltic salmon (Salmo salar) parr. Can. J. Zool. 70, 205-211.

Berglund, I., 1995. Effects of size and spring growth on sexual maturation in 1+ Atlantic salmon (Salmo salar) male parr: Interactions with smoltification. Can. J. Fish. Aquat. Sci. 52, 2682-2694.

Berrill, I. K., Porter, M. J. R., Smart, A., Mitchell, D., Bromage, N. R., 2003. Photoperiodic effects on precocious maturation, growth and smoltification in Atlantic salmon, Salmo salar. Aquaculture 222, 239-252.

Birt, T.P., Green, J.M., 1986. Parr-smolt transformation in female and sexually mature male anadromous and nonanadromous Atlantic salmon, Salmo salar. Can. J. Fish. Aquat. Sci. 43, 680-686.

Bromage, N.R., Elliott, J.A.K., Springate, J.R.C., Whitehead, C., 1984. The effects of

constant photoperiods on the timing of spawning in the rainbow trout. Aquaculture 43, 213-223.

Dalley, E.L., Andrews, C.W., Green, J.M., 1983. Precocious male Atlantic salmon parr (Salmo salar) in Insular Newfoundland. Can. J. Fish. Aquat. Sci. 40, 647-652.

Duncan, N.J., Auchinachie, N., Robertson, D., Murray, R., Bromage, N., 1998. Growth, maturation and survival of out-of-season 0+ and 1+ Atlantic salmon (Salmo salar) smolts. Aquaculture 168, 325-339.

Duncan, N.J., Bromage, N.R., 1998. The effect of different periods of constant short day on smoltification in juvenile Atlantic salmon (Salmo salar). Aquaculture 168, 369-386.

Duston, J., Bromage, N.R., 1986. Photoperiodic mechanisms and rhythms of reproduction in the female rainbow trout. Fish Physiol. Biochem. 2, 35-51.

Duston, J., Saunders, R.L., 1992. Effect of 6-, 12-, and 18-month photoperiod cycles on smolting and sexual maturation in juvenile Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci. 49, 2273-2280.

Duston, J., Saunders, R.L., 1995. Advancing smolting to autumn in age 0+ Atlantic salmon by photoperiod, and long-term performance in sea water. Aquaculture 135, 295-309.

Duston, J., Saunders, R.L., 1997. Life history of Atlantic salmon altered by winter temperature and summer rearing in fresh- or sea-water. Environ. Biol. Fish. 50, 149-166.

Elson, P.F., 1957. The importance of size in the change from parr to smolt in Atlantic

salmon. Can. Fish Cult. 21, 1-6.

Fowler, J., Cohen, L., 1987. Statistics for Ornithologists. British Trust for Ornithology, Guide 22.

Handeland, S.O., Stefansson, S.O., 2001. Photoperiod control and influence of body size on off-season parr-smolt transformation and post-smolt growth. Aquaculture 192, 291-307.

Kristinsson, J.B., Saunders, R.L., Wiggs, A.J., 1985. Growth dynamics during the development of bimodal length-frequency distribution in juvenile Atlantic salmon (Salmo salar L.). Aquaculture 45, 1-20.

McCormick, S.D., 1993. Methods for nonlethal gill biopsy and measurement of Na^+, K^+-ATPase activity. Can. J. Fish. Aquat. Sci. 50, 656-658.

Metcalfe, N. B., 1998. The interaction between behaviour and physiology in determining life history patterns in Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci. 55 (Suppl. 1), 93-103.

Miwa, S., Inui, Y., 1986. Inhibitory effects of 17α-methyltestosterone and estradiol-17β on smoltification of sterilized amago salmon (Oncorhynchus rhodurus). Aquaculture 53, 21-39.

Naevdal, G., 1983. Genetic factors in connection with age at maturation. Aquaculture 33, 97-106.

Rowe, D.K., Thorpe, J.E., 1990. Differences in growth between maturing and non-maturing male Atlantic salmon, Salmo salar L. parr. J. Fish Biol. 36, 643-658.

Saunders, R.L., Harmon, P.R., Knox, D.E., 1994. Smolt development and subsequent sexual maturity in previously mature male Atlantic salmon (Salmo salar). Aquaculture 121, 79-93.

Saunders, R.L., Henderson, E.B., Glebe, B.D., 1982. Precocious sexual maturation and smoltification in male Atlantic salmon (Salmo salar). Aquaculture 28, 211-229.

Sigholt, T., Staurnes, M., Jakobsen, H.J., Asgard, T., 1995. Effects of continuous light and short-day photoperiod on smolting, seawater survival and growth in Atlantic salmon (Salmo salar). Aquaculture 130, 373-388.

Skilbrei, O.T., 1988. Growth pattern of pre-smolt Atlantic salmon (Salmo salar L.): the percentile increment method (PIM) as a new method to estimate length-dependant growth. Aquaculture 69, 129-143.

Skilbrei, O.T., 1991. Importance of threshold length and photoperiod for the development of bimodal length-frequency distribution in Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci. 48, 2163-2172.

Solbakken, V. A., Hansen, T., Stefansson, S. O., 1994. Effects of photoperiod and temperature on growth and parr-smolt transformation in Atlantic salmon (Salmo salar L.) and subsequent performance in seawater. Aquaculture 121, 13-27.

Thorpe, J.E., 1977. Bimodal distribution of length of juvenile Atlantic salmon (Salmo salar L.) under artificial rearing conditions. J. Fish Biol. 11, 175-184.

Thorpe, J.E., 1994. Reproductive strategies in Atlantic salmon, Salmo salar L. Aquacult. Fish. Manage. 25, 77-87.

Thorpe, J. E., Mangel, M., Metcalfe, N. B., Huntingford, F. A., 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon Salmo salar L. Evol. Ecol. 12, 581-599.

Thorpe, J.E., Morgan, R.I.G., 1980. Growth-rate and smolting-rate of progeny of male Atlantic salmon parr, Salmo salar. J. Fish Biol. 17, 451-459.

Zar, J.H., 1999. Biostatistical analysis. 4th Ed., Prentice Hall: Upper Saddle River, New Jersey. 662pp.

Fig. 1. Changes in weight of Atlantic salmon parr that were exposed to different short day photoperiod treatments (LD10:14) in an otherwise continuous light regime. Weights are those recorded prior to PIT tagging in mid August (mean ± S.E.M., n=2). Differences in lettering denotes statistical differences ($P<0.05$). Lettering has been stacked in the same order as the graph lines.

Fig. 2. Changes in weight of each of four cohorts of individually PIT-tagged Atlantic salmon parr exposed to different short day photoperiods (LD10:14) in an otherwise continuous light regime. Cohorts were determined at the conclusion of the experiment in March 2002. The figure compares within cohort differences between the treatments (mean ± S.E.M., n=150-200). Differences in lettering denotes statistical differences ($P<0.05$). Lettering has been stacked in the same order as the graph lines.

Fig. 3. Changes in weight of four cohorts of individually PIT-tagged Atlantic salmon parr exposed to different short day photoperiods (LD10:14) in an otherwise continuous light regime. Cohorts were determined at the conclusion of the experiment in March 2002. The figure compares between cohort differences within each treatment (mean ± S.E.M., n=150-200). Differences in lettering denotes statistical differences ($P<0.05$). Lettering has been stacked in the same order as the graph lines.

Fig. 4. Changes in condition factor of four cohorts of individually PIT-tagged Atlantic salmon parr exposed to different short day photoperiods (LD10:14) in an otherwise continuous light regime (mean ± S.E.M., n=150-200). Cohorts were determined at the conclusion of the experiment in March 2002. Differences in lettering denotes statistical differences ($P<0.05$). Lettering has been stacked in the same order as the

graph lines.

Fig. 5. Changes in the percentage maturation of Atlantic salmon parr exposed to different short day photoperiods (LD10:14) in an otherwise continuous light regime (n=400-1400). Differences in lettering denotes statistical differences ($P<0.05$). Lettering has been stacked in the same order as the graph lines.

Fig. 6. Changes in the gill Na^+, K^+-ATPase activities of Atlantic salmon parr exposed to different short day photoperiods (LD10:14) in an otherwise continuous light regime (mean ± S.E.M., n=20). The ATPase activities of fish showing signs of silvering and those without silvering have been separated to aid interpretation. The weights (mean ± S.E.M., n=20) of fish sampled have also been represented. Differences in lettering denotes statistical differences ($P<0.05$). Statistical differences in the weight data have been omitted to improve the clarity of the figure.

Fig. 1

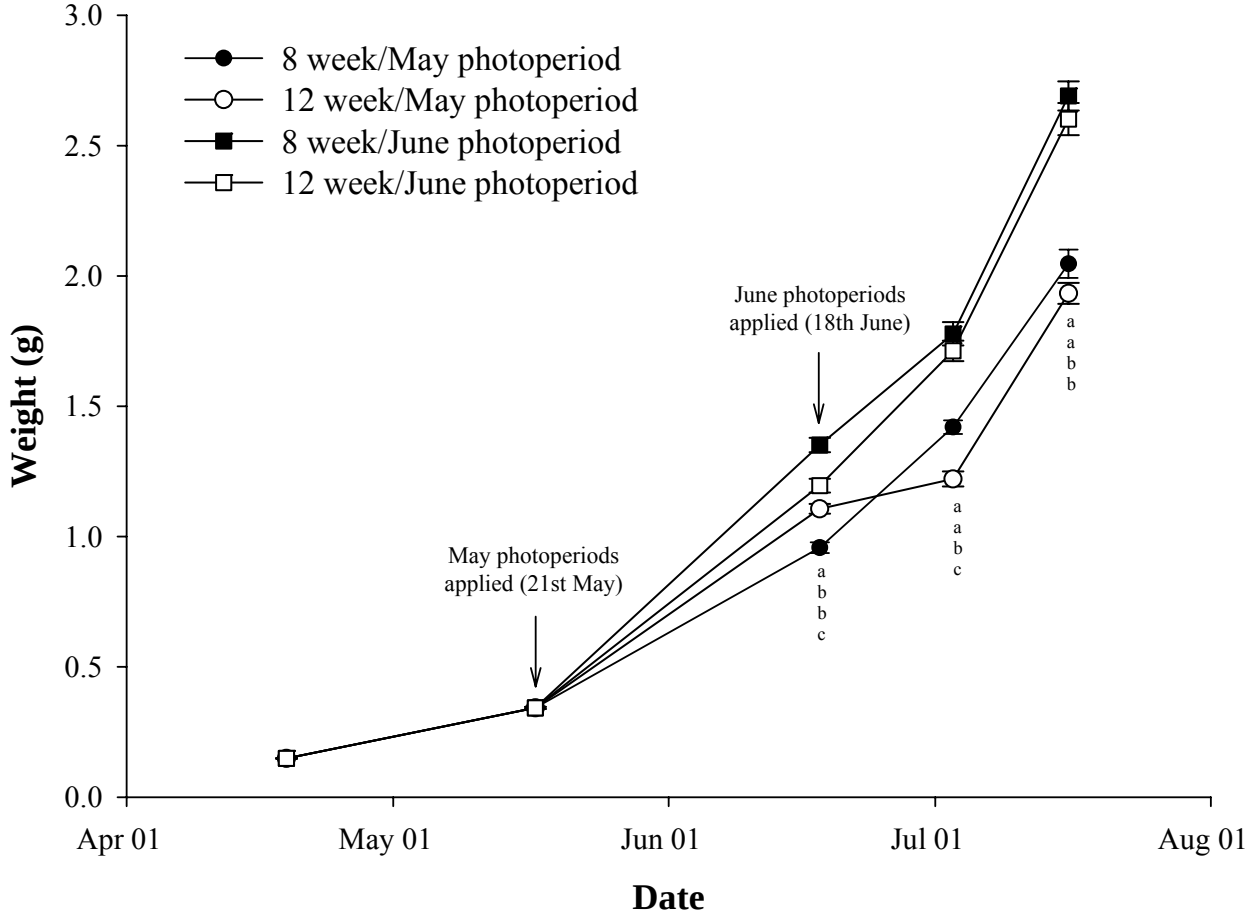
8 week/May photoperiod
12 week/May photoperiod
8 week/June photoperiod
12 week/June photoperiod
Weight (g)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Apr 01
May 01
Jun 01
Jul 01
Aug 01
Date
May photoperiods
applied (21st May)
June photoperiods
applied (18th June)
a
b
b
c
a
a
b
c
a
a
b
b

Fig. 2

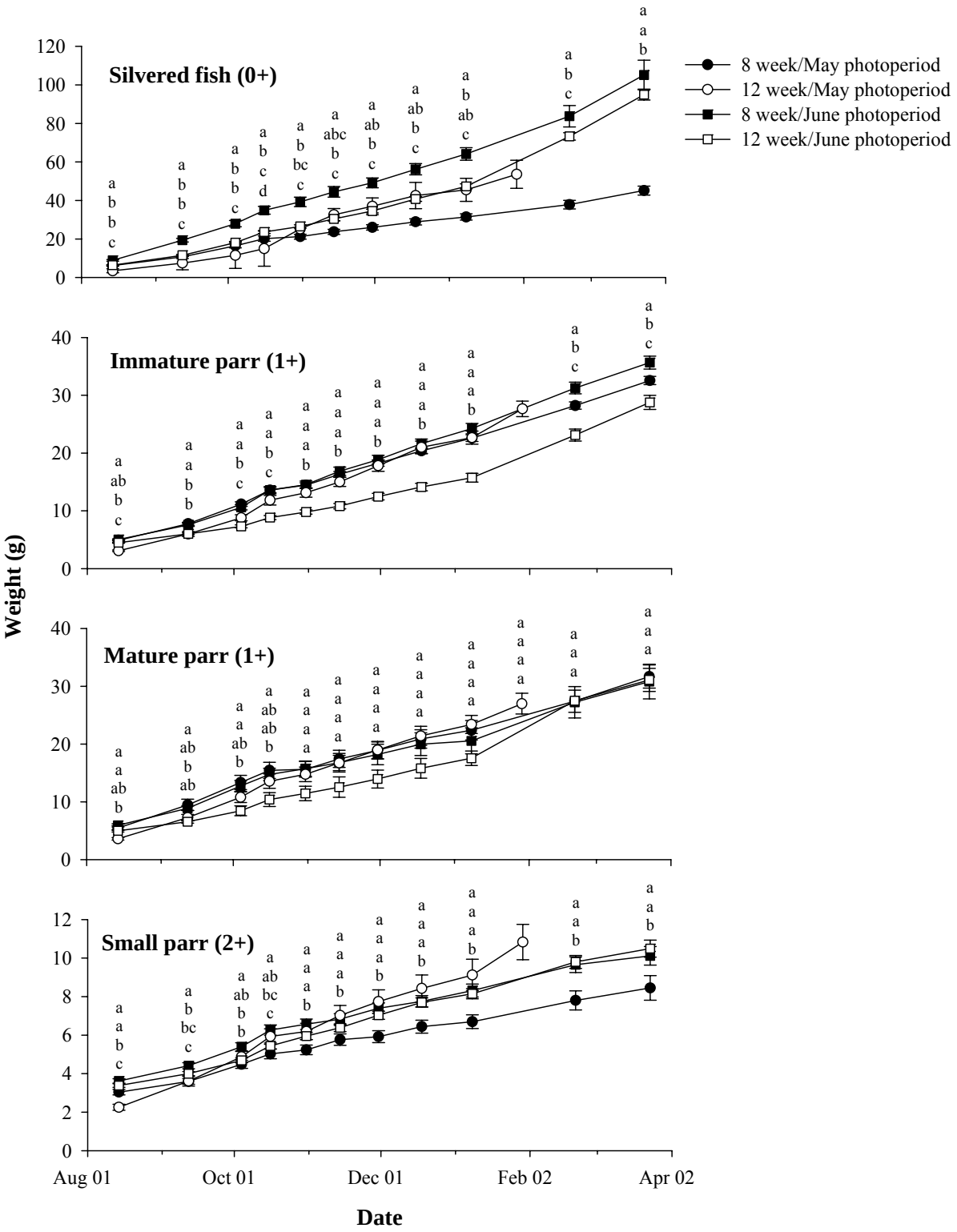
Silvered fish (0+)
Immature parr (1+)
Mature parr (1+)
Small parr (2+)
8 week/May photoperiod
12 week/May photoperiod
8 week/June photoperiod
12 week/June photoperiod
Weight (g)
Aug 01
Oct 01
Dec 01
Feb 02
Apr 02
Date

Fig. 3

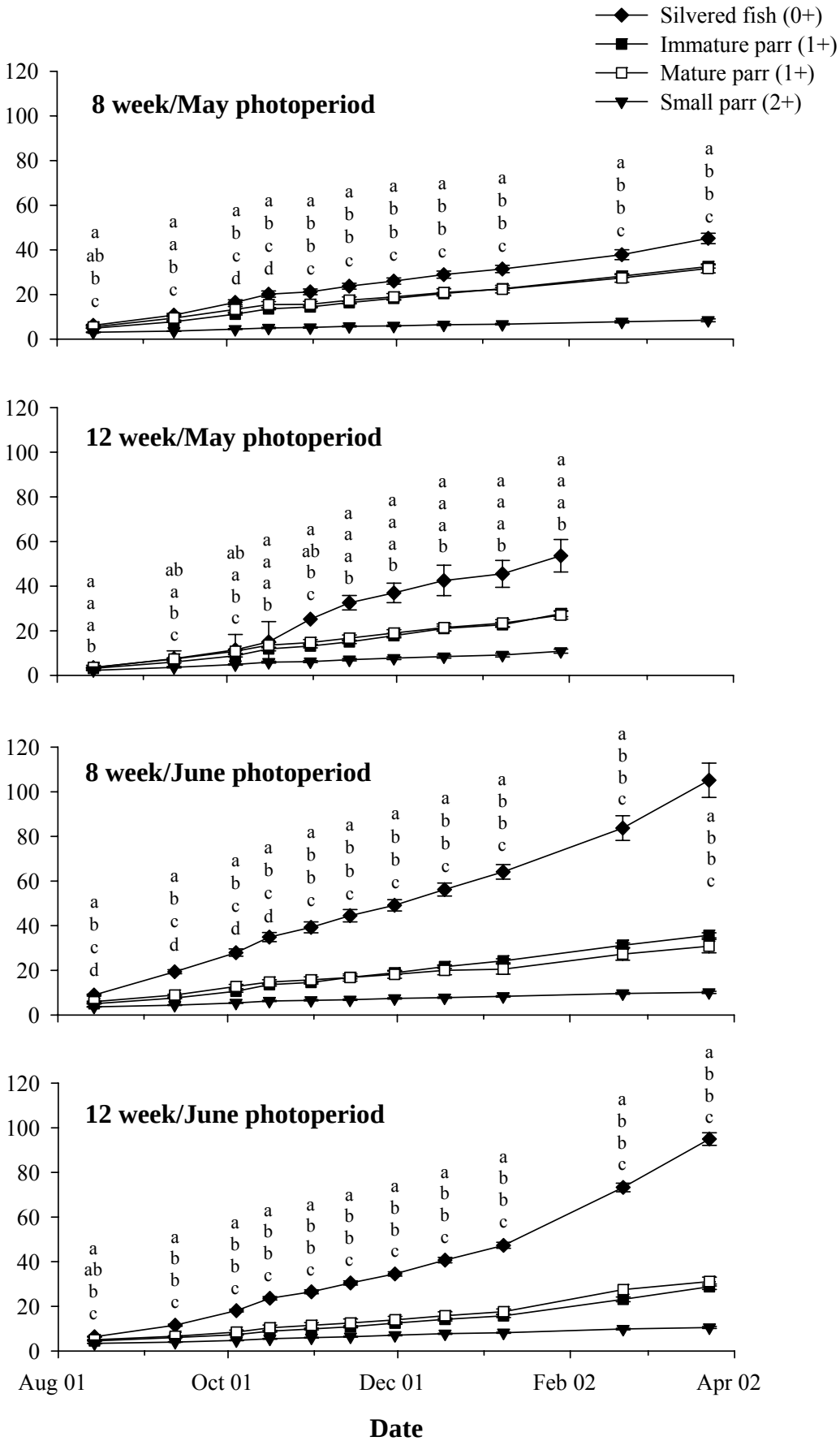
Silvered fish (0+)
Immature parr (1+)
Mature parr (1+)
Small parr (2+)
8 week/May photoperiod
12 week/May photoperiod
8 week/June photoperiod
12 week/June photoperiod
0
20
40
60
80
100
120
Aug 01
Oct 01
Dec 01
Feb 02
Apr 02
Date

Fig. 4

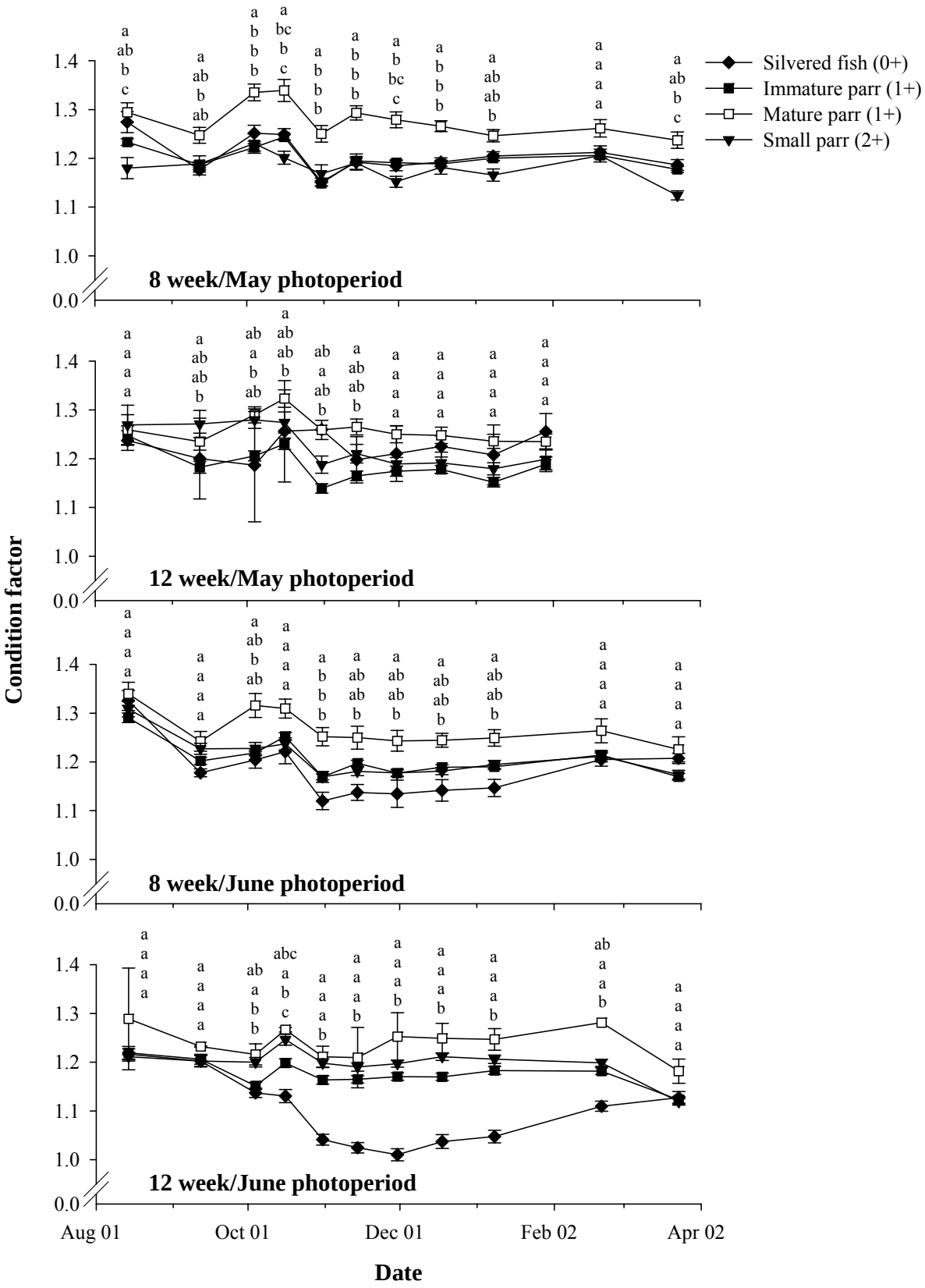
Silvered fish (0+)
Immature parr (1+)
Mature parr (1+)
Small parr (2+)
8 week/May photoperiod
12 week/May photoperiod
8 week/June photoperiod
12 week/June photoperiod
Condition factor
Date
Aug 01
Oct 01
Dec 01
Feb 02
Apr 02

Fig. 5

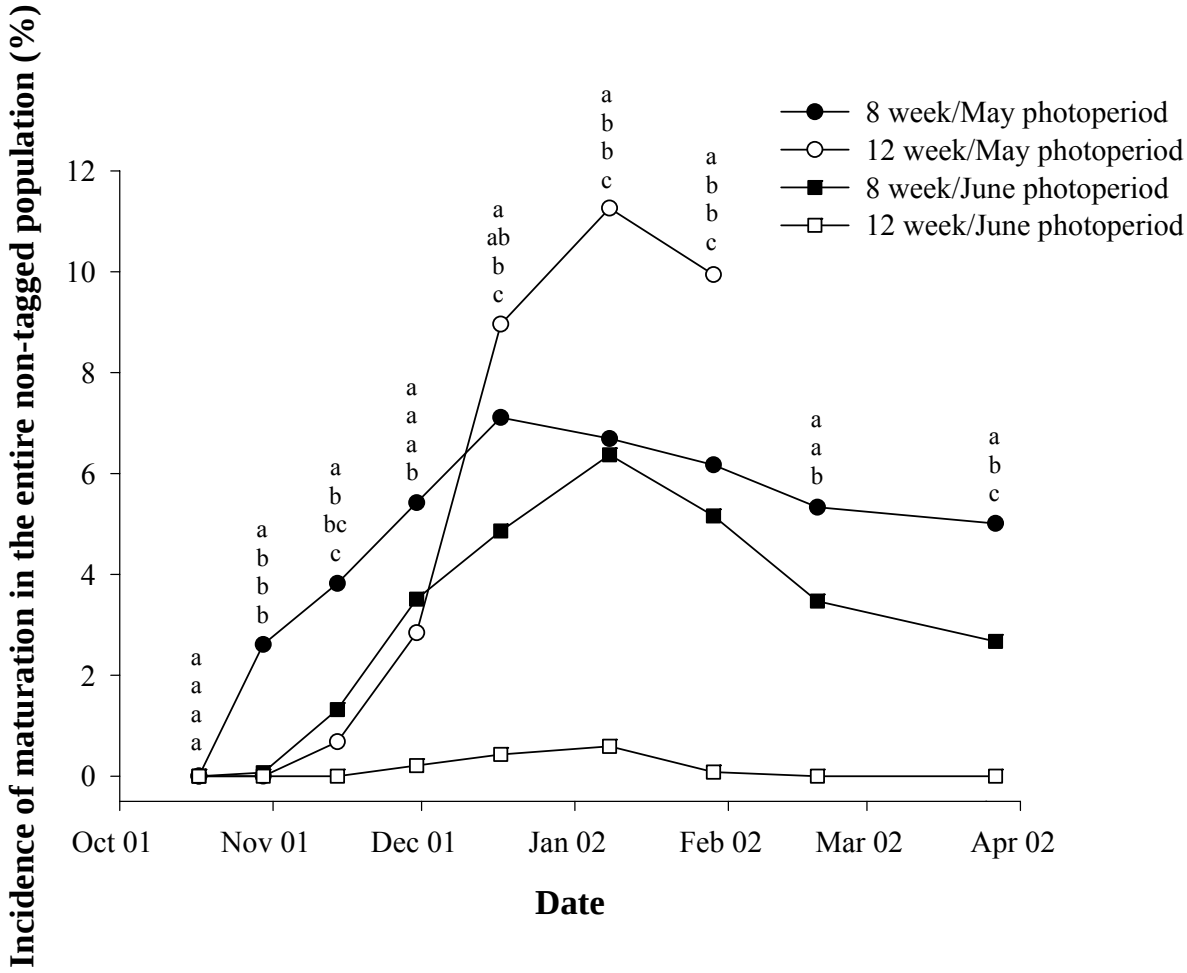
Incidence of maturation in the entire non-tagged population (%)
12
10
8
6
4
2
0
Oct 01
Nov 01
Dec 01
Jan 02
Feb 02
Mar 02
Apr 02
Date
8 week/May photoperiod
12 week/May photoperiod
8 week/June photoperiod
12 week/June photoperiod
a a a a
a b b b
a b bc c
a a a b
a ab b c
a b b c
a b b c
a a b
a b c

Fig. 6

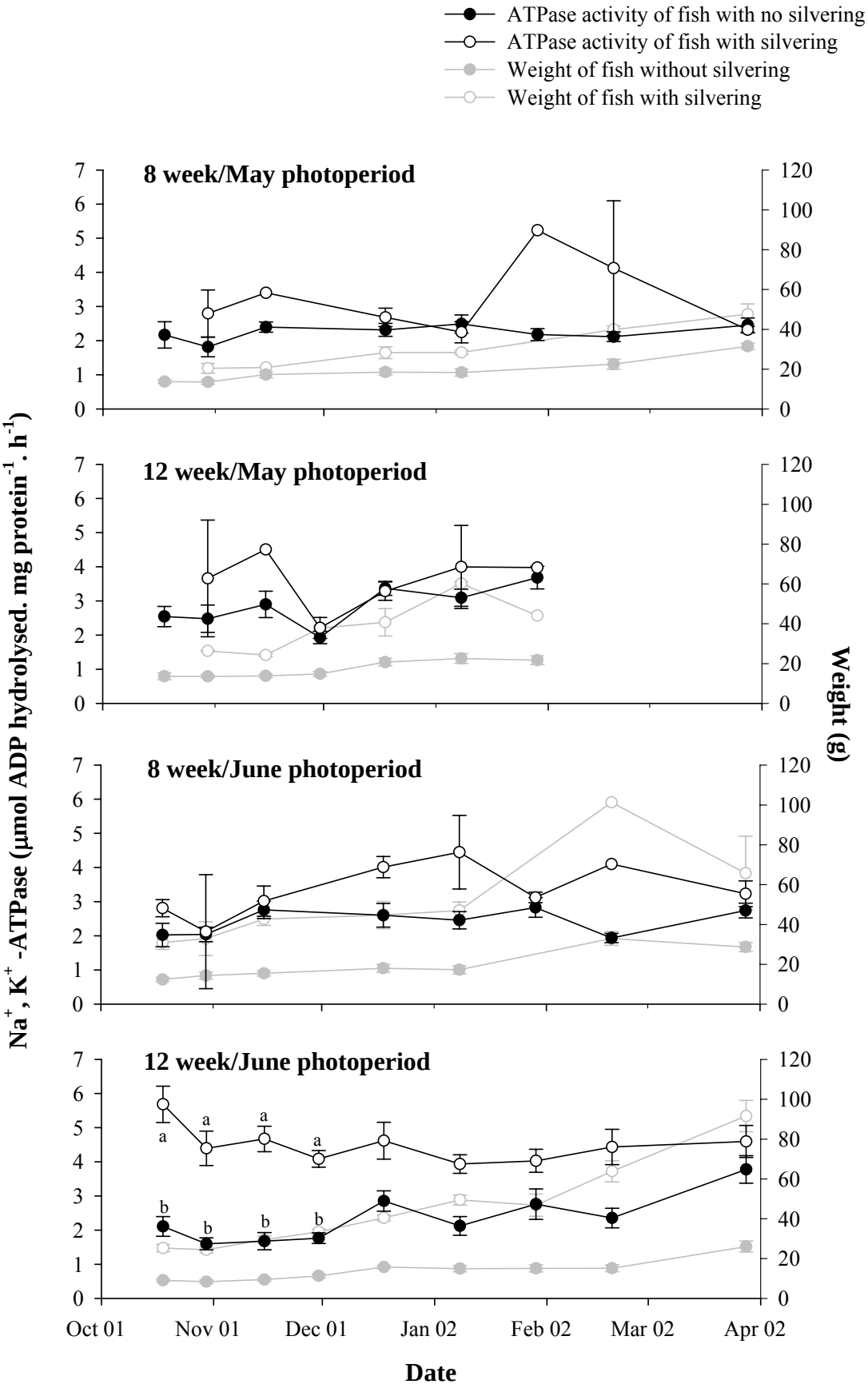
ATPase activity of fish with no silvering
ATPase activity of fish with silvering
Weight of fish without silvering
Weight of fish with silvering
8 week/May photoperiod
12 week/May photoperiod
8 week/June photoperiod
12 week/June photoperiod
Na+, K+ -ATPase (µmol ADP hydrolysed. mg protein-1 . h-1)
Weight (g)
Oct 01
Nov 01
Dec 01
Jan 02
Feb 02
Mar 02
Apr 02
Date

Table 1. The start and end dates of the four experimental short day photoperiod regimes (LD10:14) used in the current study. At all other times fish were exposed to continuous light (LD24:0).

Experimental regime	LD10:14 photoperiod regime	
	Start date	End date
8 week/May photoperiod	18th May	16th July
12 week/May photoperiod	18th May	14th August
8 week/June photoperiod	21st June	14th August
12 week/June photoperiod	21st June	12th September

Table 2. Population structure at the conclusion of an experiment in which Atlantic salmon parr were exposed to different short day photoperiods (LD10:14) in an otherwise continuous light (LD24:0) regime. The population structure was based on the external appearance of 150 non-tagged individuals per treatment. Refer to Materials and Methods for details of cohort nomenclature. Different lettering denotes statistical differences ($P<0.05$). Capital lettering denotes between cohort differences within a treatment. Lower case lettering denotes between treatment differences, within a cohort.

	8 week/May photoperiod	12 week/May photoperiod	8 week/June photoperiod	12 week/June photoperiod
Silvered fish (0+)	4.1% ^{Aa}	3.7% ^{Aa}	7.5% ^{Aa}	30.2% ^{Ab}
Immature parr (1+)	67.6% ^{Ba}	61.9% ^{Ba}	65.3% ^{Ba}	34.5% ^{Ab}
Mature parr (1+)	12.8% ^{ACab}	20.9% ^{Ca}	12.9% ^{Aab}	4.3% ^{Bb}
Small parr (2+)	15.5% ^{Cab}	13.4% ^{Ca}	14.3% ^{Aa}	30.9% ^{Ab}