1 TIMING AND DURATION OF CONSTANT LIGHT AFFECTS RAINBOW TROUT

2 (*ONCORHYNCHUS MYKISS*) GROWTH DURING AUTUMN-SPRING GROW-OUT IN

3 FRESHWATER

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13 **Keywords**

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Abstract

Photoperiod enhancement of growth is becoming an area of increasing interest as a means of enhancing rainbow trout production efficiency in commercial practice. This paper examines the possible implications of shortening periods of constant light (LL) exposure on rainbow trout growth during autumn-spring grow out under ambient water temperatures in freshwater to portion size. Triplicate groups of juvenile all-female rainbow trout were permanently exposed to LL in October, November, December or January. Growth was monitored and compared to those maintained under a simulated natural photoperiod (SNP) until the following May. Permanent exposure to LL (all treatments) resulted in significantly greater weight gain of rainbow trout than those under SNP. Furthermore, greatest growth was achieved when fish were left permanently exposed to LL from October. These findings suggest there may be implications for fish farmers if the period of photoperiod exposure is reduced, or timing of application is not considered with regards to ambient water temperatures.

Introduction

Previous trials have demonstrated that exposure of juvenile rainbow trout (*Oncorhynchus mykiss*) to periods of constant light (LL) or long-days can significantly improve growth rates relative to those maintained under ambient conditions (Mason, Gallant, & Wood, 1991; Makinen & Ruhonen, 1992; Taylor, North, Porter, Bromage, & Migaud, 2006). However, the duration of LL and the actual timing of exposure to LL has not yet been determined in relation to optimising growth enhancement during autumn-spring grow-out in portion size rainbow trout in freshwater. It has been clearly shown in

39   Atlantic salmon (*Salmo salar*) that the longer the exposure to LL, the longer the period that

40   higher growth rates will be maintained, suggesting a direct photostimulation of growth

41   (Taranger, Haux, Hansen, Stefansson, Bjornsson, Walther & Kryvi, 1999; Endal, Taranger,

42   Stefansson & Hansen, 2000). However, it was also evident that enhanced growth was

43   maintained after salmon were returned to natural photoperiod following LL application

44   suggesting that photoperiod is adjusting seasonal growth and appetite rhythms, rather than

45   as a consequence of direct photostimulation (Kadri, Metcalfe, Huntingford & Thorpe, 1997;

46   Nordgarden, Oppedal, Hansen & Hemre, 2003; Oppedal, Berg, Olsen, Taranger, & Hansen,

47   2006). If direct photostimulation of growth does occur then the stimulatory effect would

48   last only as long as additional light was applied (Johnston, Manthri, Smart, Campbell,

49   Nickell & Alderson, 2003). However, more recently it has been demonstrated in Atlantic

50   salmon that muscle fibre recruitment is enhanced following initial LL application in autumn

51   rather than muscle hypertrophy. It was also postulated that the earlier the onset of LL the

52   greater the effect on recruitment there may be. Once recruitment ceases, growth occurred

53   only via hypertrophy of fibres previously formed (Johnston, et al., 2003; Johnston, Manthri,

54   Bickerdike, Dingwall, Luijkx, Campbell, Nickell & Alderson, 2004).

55   Temperature has been shown to act synergistically with photoperiod in a rate-

56   controlling manner on growth response following photoperiod manipulation in numerous

57   species (Clarke, Shelbourn & Brett, 1978; Solbakken, Hansen & Stefansson, 1994;

58   Hallaraker, Folkvord & Stefansson, 1995; Jonassen, Imsland, Kadowaki & Stefansson,

59   2000). This is particularly important with regards to the use of photoperiod regimes during

60   the winter period in which temperature may limit the physiological response. In juvenile

61   Atlantic salmon, and both underyearling coho and sockeye salmon the growth response

62 during photoperiod manipulation was greater at higher temperatures in autumn (Clarke *et*

63 *al*. 1978; Clarke, Shelbourn & Brett, 1981; Saunders, Specker & Komourdjian, 1989).

64 Thorpe, Adams, Miles & Keay, (1989) suggested a greater opportunity for growth as

65 represented by degree-daylight hours in mid to late summer, in which a greater proportion

66 of juvenile salmon would maintain rather than arrest growth. Similar responses have been

67 observed in Atlantic salmon whereby increasing day-lengths did not enhance growth when

68 temperatures were low, while artificially elevating temperatures during late winter and

69 early spring in association with exposure to LL successfully enhanced growth (Saunders,

70 Henderson & Harmon, 1985; Solbakken *et al*. 1994). This rate-controlling regulation may

71 relate in part to the modulatory effect of the somatotropic axis hormones (GH-IGF-I) which

72 have been shown to be influenced by temperature (Beckman, Larsen, Moriyama, Lee-

73 Pawlak & Dickhoff, 1998; Larsen, Beckman & Dickhoff, 2001) in addition to feed intake

74 (Pierce, Beckman, Shearer, Larsen & Dickhoff, 2001; Beckman, Shimizu, Gadberry &

75 Cooper, 2004) and photoperiod (McCormick, Moriyama & Bjornsson, 2000; Taylor,

76 Migaud, Porter & Bromage, 2005). Thus the timing of photoperiod application and the

77 subsequent response should be given careful consideration with regards to ambient

78 temperatures.

79   At present, the UK trout industry does not employ lighting regimes in portion-size

80 fish. However, there is a growing interest in the potential to use artificial lighting to

81 promote growth during autumn-spring grow out, a period associated with naturally poor

82 performance under ambient conditions (Taylor *et al*. 2006), and thus use light to increase

83 productivity. Evaluation of such approaches could provide simple and cost effective means

84 which could be applied within the industry, and furthermore, may add to the limited

85 knowledge of the physiological effects of photoperiod manipulation on the mechanisms

86 controlling trout growth. In this respect, this paper examines implications of different

87 timing of exposure and duration of LL application on growth performance of rainbow trout

88 during autumn to spring grow-out.

89

90 **Materials and methods**

91 On 24th October 2002 groups of 50 all-female rainbow trout (90.0 ± 1.6g, mean ±

92 SEM, Glen Wyllin origin, hatch May 2001) previously reared under natural photoperiod

93 and water temperature (2.3-15°C) were exposed to one of 5 photoperiod treatments in

94 triplicate. One triplicate group was maintained under simulated natural photoperiod (SNP:

95 range 7-17.25 hours daylight) as a control treatment throughout the experiment. The

96 remaining four triplicate groups were exposed to constant light (LL) on 24th October (LL-

97 OCT), 20th November (LL-NOV), 18th December (LL-DEC) and 20th January (LL-JAN)

98 until 26th May 2003 (Figure. 1).

99 The experiment was conducted at the Niall Bromage Freshwater Research Facility

100 (52°30'N) with freshwater supplied to all tanks by gravity from an upstream reservoir. Fish

101 were reared in 1.38m^3 circular flow-through fibreglass tanks (start SD 16kg/m^3). Flow rates

102 to all tanks were maintained at 10L sec^{-1} with DO maintained above 7mg L^{-1}, pH 6.5-6.8,

103 and ambient water temperature (Fig. 1). Light was supplied by two 9 watt equivalent G23

104 bulbs (RS components Ltd., Northants, UK) housed in one aluminium alloy bulkhead

105 fittings positioned centrally in the lightproof lid creating 0.2 Wm^{-2} on the tank floor.

106 Simulated natural photoperiod regimes were controlled using a photosensitive switch (RS

107 Components Ltd., Northants, UK), while lighting to LL tanks was permanently switched

5

108   on. Fish in all treatments were fed a commercial dry diet (Trouw Elips-S 4mm pellet) to

109   satiation (0.5% above recommended feeding tables) via automated feeders during the

110   daylight hours of the SNP treatment with all treatments presented an identical ration,

111   however direct feed intake through waste feed collection was not determined.

112   All fish from all treatments (n=48-50) were anesthetised with 2-phenoxyethanol

113   (1:10,000 dilution, Sigma, UK), individually measured for weight (W) ($\pm$ 0.1g) and fork

114   length (L) ($\pm$ 0.5mm) at monthly intervals, recovered in well aerated water and returned to

115   their respective photoperiod treatment tank. Condition factor (K) was calculated from the

116   measured length and weight of individual fish such that: $K = (WL^{-3})x100$. Mortalities were

117   less than 4% during the experiment. Specific growth rates (SGR) were calculated such that:

118    $SGR = (e^g-1) \times 100$, where $g = (Ln\underline{X}_2 - Ln\underline{X}_1) / \underline{t}_2 - \underline{t}_1$ and $\underline{X}_2$ and $\underline{X}_1$ are W or L at times $\underline{t}_2$

119   and $\underline{t}_1$ respectively. A starting SGR in October was based on the fish stock growth prior to

120   experimentation during the previous month while held at the facility.

121   Differences in growth performance (W, L, K and SGR) were analysed using a

122   nested ANOVA, in which treatment tanks were nested as a random factor within the

123   dependent factor photoperiod at a given sampling point. Data complied with normality and

124   homogeneity of variance tests. No replicate differences were found within photoperiod

125   treatments. For post-hoc multiple comparisons, Tukey's test was used with a significance

126   level of 5% ($p<0.05$). All statistical analysis were undertaken using Minitab Statistical

127   Package v14.1.

128

129   **Results**

130   All treatments increased W steadily over the duration of the trial. LL-OCT achieved

131   and maintained a significantly higher mean W than all other treatments by March 2003

132   (Fig. 2a). LL-NOV, LL-DEC, and LL-JAN treatments reached a significantly heavier

133   weight than SNP by April 2003 that was maintained until the end of the experiment (Fig.

134   2a), concurrent with a significantly higher SGR during this period with the exception of

135   LL-JAN (Fig. 2b). Overall weight gain advantage relative to SNP final weight in May was

136   21% for LL-OCT and 11% for LL-NOV, LL-DEC, and LL-JAN treatments respectively.

137   L increased steadily in all treatments throughout the experiment, with all LL

138   exposures achieving a significantly longer L than SNP during May 2003, with no

139   differences between LL treatments apparent (data not shown).

140   In general, weight SGR followed a similar pattern in LL and SNP treatments,

141   showing a significant decrease from October to November 2002, concurrent with the rapid

142   fall in temperature, before slowly increasing from November to February 2003 (Fig. 2b).

143   Between March and May 2003 SGR increased steeply in all LL treatments with LL-OCT,

144   LL-NOV, LL-DEC achieving a significantly higher SGR than SNP in April. In May all LL

145   treatments achieved a significantly higher SGR than SNP.

146   All treatments maintained a steady K between October and November, which was

147   followed by a dramatic decrease in all groups in December 2002 (Fig. 2c). The control SNP

148   then showed a gradual increase in K from December 2002 to March 2003, followed by a

149   decrease in April, only to rise again during May. K in both LL-OCT and LL-NOV

150   increased between December and February achieving a significantly higher K value than

151   SNP, but not in the LL-DEC or LL-JAN groups. K in both treatments then increased

152   through April and May achieving a significantly higher K than SNP. Fish in LL-DEC and

153   LL-JAN groups only displayed a significantly higher K value than SNP in April and May.

154   Significant differences in K were not apparent between any of LL treatments in April or

155   May.

156

157   **Discussion**

158   The present study provides clear evidence that abrupt changes from natural

159   photoperiod to LL in October, November, December or January enhances weight gain of

160   portion-size rainbow trout in freshwater. Moreover, maximum growth enhancement was

161   achieved following permanent exposure to LL from October. Furthermore, although

162   conducted at an experimental level SGRs obtained in our study were representative of those

163   observed under full-scale commercial conditions (Taylor et al., 2006) suggesting our

164   findings could provide practical tools directly applicable to industry.

165   These growth enhancing effects of LL are in accordance with those previously

166   observed in juvenile and adult Atlantic salmon (Saunders *et al*. 1985; Stefansson, Naevdal

167   & Hansen, 1989; Solbakken *et al*. 1994; Oppedal, Taranger, Juell, Fosseidengen & Hansen,

168   1997), Pacific salmonids (Clarke 1990), and provides further support to the limited

169   knowledge of photoperiod effects on growth in rainbow trout (Mason *et al*. 1991; Makinen

170   & Ruhonen 1992; Taylor *et al*. 2005). However, care must be taken when drawing

171   comparisons between rainbow trout and other salmonid species, in particular freshwater

172   and post-smolt stages. The use of LL from autumn-winter through to June in Atlantic

173   salmon culture is an industry standard principally used to inhibit early maturation pre-

174   harvest (Hansen, Stefansson & Taranger, 1992; Hansen, Stefansson, Taranger, & Norberg,

175   2000), the subsequent effect being the reallocation of energy from gonadal development

176   into somatic tissue growth. This however is not an issue in all-female portion-size rainbow

177   trout production (250-300g) which do not typically mature at this size. Although maturity

178   was not assessed in the current experiment, we have extensively used this strain in other

179   studies and observe no maturity before 3years old in females. Equally it is difficult to

180   dissociate growth from smoltification when looking at freshwater stages of salmon

181   (Skilbrei, Hansen & Stefansson, 1997; Duncan & Bromage, 1998).

182   Nonetheless, our study suggests that the earlier the exposure and the longer the

183   duration of LL in rainbow trout, the greater the degree of enhanced growth, supporting a

184   direct photostimulation of growth theory. Similarly, in Atlantic salmon it was shown that

185   longer exposure maintains a higher growth rate for a longer period (Taranger *et al*. 1999;

186   Endal *et al*. 2000). Oppedal, Taranger, Juell & Hansen, (1999) also found no difference in

187   the pattern or rate of growth in underyearling Atlantic salmon exposed to LL for a short

188   period of time, 12 weeks, whereas a previous study only observed an effect 18 weeks post-

189   light exposure (Oppedal, *et al*. 1997). It has been proposed that fish are unable to

190   synchronise their endogenous rhythms under rapidly increasing and decreasing artificial

191   photoperiod (Clarke et al. 1978; Villarreal, Thorpe & Miles, 1988). Certainly the earlier

192   application in October in conjunction with the greatest growth could suggest a phase shift

193   relative to the other LL treatments, yet no differences in growth were observed between the

194   other LL treatments although they did achieve a larger weight than the SNP treatment. In

195   this respect our data does not support the idea of an endogenous rhythm of growth in

196   rainbow trout although further studies are needed to clarify the situation. Conversely,

197   Nordgarden et al., (2003) reported a clear seasonal profile of growth, condition and feed

198   intake in Atlantic salmon, and that improved growth under LL was associated with

199 improved FCR and increased appetite. As such both FCR and feed intake should be

200 monitored accurately in future trials under the given light treatments in order to draw firm

201 conclusions with regards to rainbow trout. Although waste feed was not monitored in our

202 study, fish were fed to excess and differences in growth due to under-feeding would seem

203 unlikely.

204   Regarding changes in length no significant differences were observed between LL

205 treatments and SNP despite the former treatments achieving significantly greater weights.

206 Only during the May did LL groups achieve a greater length than SNP. As a result, LL

207 treated fish achieved significantly higher K factors than SNP in spring. Seasonal growth

208 patterns under endogenous control which can be manipulated by light treatment have been

209 demonstrated in Atlantic salmon (Nordgarden *et al*. 2003; Oppedal, et al., 2006). Typical

210 patterns have shown a tendency towards greater skeletal growth during the winter months,

211 providing the frame for muscle gain in spring (Björnsson et al., 2000). In this respect,

212 Johnston *et al*. (2003) reported significantly enhanced weight gain of Atlantic salmon 18

213 weeks post LL exposure. A shift towards greater muscle fibre recruitment was observed

214 during the first 40 days of LL exposure, subsequently followed by muscle hypertrophy.

215 Interestingly within our study, LL-OCT and LL-NOV achieved a significantly higher K

216 before LL-DEC and LL-JAN treatments, suggesting greater muscle gain given that

217 treatments were of the same length during this period. This difference could relate to a

218 longer period of muscle fibre recruitment following the earlier application of light. A future

219 study examining muscle fibre dynamics may reveal the underlying mechanism in rainbow

220 trout.

221   Finally, in the present study, greatest weight gain was observed in LL applied as of

222   October relative to all other LL treatments. Together with the possible involvement of a

223   phase advancement of a seasonal growth pattern, the greater growth may also be explained

224   by the higher water temperatures at which the light regime was initially applied (12ºC in

225   Oct versus 2-4ºC Nov-Jan). Since fish are ectothermic, then many of their physiological

226   processes are regulated by the thermal regime, with optimum ranges for a variety of

227   freshwater and marine species (Saunders *et al*. 1985; Solbakken *et al*. 1994; Hallaraker, *et*

228   *al*. 1995; Jonassen, *et al*. 1999). Numerous studies have shown that changes in growth rate

229   caused by photoperiod treatment in other salmonids were apparent sooner at higher

230   temperatures than at lower ones (Clarke *et al*. 1978; Clarke *et al*. 1981; Saunders *et al*.

231   1985; Solbakken *et al*. 1994). Thus, temperature is considered as a rate-controlling factor,

232   whereas light would be classified as a directive factor that stimulates the endocrine system

233   (Bromage, Randall, Duston, Thrush & Jones, 1994). More rapid increases in circulating GH

234   and IGF-I have been found in relation to higher temperatures (Beckman *et al*. 1998; Larsen

235   *et al*. 2001) and increasing or long-day photoperiods (Björnsson 1997; McCormick *et al*.

236   2000; Taylor *et al*. 2005). Therefore, since GH and IGF-I in particular, are known potent

237   stimulators of muscle growth (McCormick, Kelley, Young, Nishioka & Bern, 1992), then

238   the greater weight gain we observed following earlier application of photoperiod in October

239   in conjunction with higher water temperatures may simply relate to greater muscle

240   recruitment and growth as previously postulated by Johnston *et al*. (2003). This would

241   certainly conform with the greater K factors achieved in spring. Unfortunately, no muscle

242   fibre or GH/IGF analysis was performed in the current experiment and should certainly be

243   included in future studies in this field to determine the physiological mechanisms that are

244 contributing to growth. Similarly, in future a trial but under constant temperature conditions

245 may also be able to differentiate the effects of temperature from photoperiod on seasonal

246 patterns of growth.

247   In summary, these results provide useful information for the rainbow trout industry

248 to capitalise on in order to enhance production efficiency, and indicate avenues by which

249 knowledge of the physiological mechanisms underlying rainbow trout growth could be

250 expanded.

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259 **References**

260 Beckman B.R., Larsen D.A., Moriyama S., Lee-Pawlak B. & Dickhoff W.W. (1998)

261   Insulin-like growth factor-I and environmental modulation of growth during

262   smoltification of spring chinook salmon (*Oncorhynchus tshawytscha*). *General and*

263   *Comparative Endocrinology* **109**, 325-335.

264 Beckman B.R., Shimizu M., Gadberry B.A. & Cooper K.A. (2004) Response of the

265   somatotropic axis of juvenile coho salmon to alterations in plane of nutrition with

266   an analysis of the relationships among growth rate and circulating IGF-I and 41 kDa

267   IGFBP. *General and Comparative Endocrinology* **135** , 334-344.

268   Björnsson B.T. (1997) The biology of salmon growth hormone: from daylight to

269   dominance. *Fish Physiology and Biochemistry* **17**, 9-24.

270   Björnsson B.T., Hemre G.-I., Bjørnevik M. & Hansen T. (2000) Photoperiod regulation of

271   plasma growth hormone levels during induced smoltification of underyearling

272   Atlantic salmon. *General and Comparative Endocrinology* **119**, 17-25.

273   Bromage N.R., Randall C.F., Duston J., Thrush M. & Jones J. (1994) Environmental

274   control of reproduction in salmonids. In *Recent Advances in Aquaculture IV*, ed.

275   Muir J.F. & Roberts, R.J., pp. 55-65. Blackwell Scientific Publications.

276   Clarke C. (1990) Light control lengthens grow-out season. *The Fish Farm News* **3**, 26

277   Clarke W.C., Shelbourn J.E. & Brett J.R. (1981) Effect of artificial photoperiod cycles,

278   temperature, and salinity on growth and smolting in underyearling coho

279   (*Oncorhynchus kisutch*), chinook (*O. tshawytscha*), and sockeye (*O. nerka*) salmon.

280   *Aquaculture* **22**, 105-116.

281   Clarke W.C., Shelbourn J.E. & Brett J.R. (1978) Growth and adaptation to sea water in

282   'underyearling' sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon

283   subjected to regimes of constant or changing temperature and day length. *Canadian*

284   *Journal of Zoology* **56**, 2413-2421.

285   Duncan N.J. & Bromage N.R. (1998) The effect of different periods of constant short days

286   on smoltification in juvenile Atlantic salmon (*Salmo salar*). *Aquaculture* **168**, 369-

287   386.

288   Endal H.P., Taranger G.L., Stefansson S.O. & Hansen T. (2000) Effects of continuous

289   additional light on growth and sexual maturity in Atlantic salmon, *Salmo salar*,

290   reared in sea cages. *Aquaculture* **191**, 337-349.

291   Hallaraker H, Folkvord A. & Stefansson S.O. (1995) Growth of juvenile halibut

292   (*Hippoglossus hippoglossus*) related to temperature, day length and feeding regime.

293   *Netherlands Journal of Sea Research* **34**, 139-147.

294   Hansen T., Stefansson S.O. & Taranger G.L. (1992) Growth and sexual maturation in

295   Atlantic salmon, *Salmo salar* L., reared in sea cages at two different regimes.

296   *Aquaculture and Fisheries Management* **23**, 275-280.

297   Hansen, T., Stefansson, S.O., Taranger, G.L., Norberg, B., (2000) Aquaculture in Norway.

298   In: Norberg, B., Kjesbu, O.S., Taranger, G.L., Andersson, E., Stefansson, S.O.

299   (Eds.), *Proceedings of the. 6th International. Symposium Reproductive Physiology*

300   *of Fish*. Institute of Marine Research and University of Bergen, Norway, 4-9 July

301   1999, Bergen, Norway,. 408-411.

302   Johnston I.A., Manthri S., Smart A., Campbell P., Nickell D. & Alderson R. (2003)

303   Plasticity of muscle fibre number in seawater stages of Atlantic salmon in response

304   to photoperiod manipulation. *Journal of Experimental Biology* **206**, 3425-3435.

305   Johnston., I.A., Manthri, S., Bickerdike, R., Dingwall, A., Luijkx, R., Campbell P, Nickell

306   D and Alderson, R. (2004) Growth performance, muscle structure and flesh quality

307   in out-of-season Atlantic salmon (*Salmo salar*) smolts reared under two different

308   photoperiod regimes. *Aquaculture* **237**, 281-300.

309   Jonassen T.M., Imsland A.K., Kadowaki S. & Stefansson S.O. (2000) Interaction of

310   temperature and photoperiod on growth of Atlantic halibut *Hippoglossus*

311   *hippoglossus* L. *Aquaculture Research* **31**, 219-227.

312   Kadri S., Metcalfe N.B., Huntingford F.A. & Thorpe J.E. (1997) Daily feeding rhythms in

313   Atlantic salmon I: feeding and aggression in parr under ambient environmental

314   conditions. *Journal of Fish Biology* **50**, 267-272.

315   Larsen D.A., Beckmann B.R. & Dickhoff W.W. (2001) The effect of low temperature and

316   fasting during the winter on metabolic stores and endocrine physiology (insulin,

317   IGF-I, and thyroxine) of coho salmon, *Oncorhynchus kisutch*. *General and*

318   *Comparative Endocrinology* **123**, 308-323.

319   Mason E. G., Gallant R. K. & Wood L. (1991) Productivity enhancement of rainbow trout

320   using photoperiod manipulation. *Bulletin of the Aquaculture Association of Canada*

321   **91**, 44-46.

322   Makinen T. & Ruhonen K. (1992) Effect of delayed photoperiod on the growth of a Finnish

323   rainbow trout (*Oncorhynchus mykiss*) stock. *Journal of Applied Ichthyology* **8**, 40-

324   50.

325   McCormick S.D., Kelley K.M., Young G., Nishioka R.S. & Bern H.A. (1992) Stimulation

326   of coho salmon growth by insulin-like growth factor-I. *General and Comparative*

327   *Endocrinology* **86**, 398-406.

328   McCormick S.D., Moriyama S. & Bjornsson B.T. (2000) Low temperature limits

329   photoperiod control of smolting in Atlantic salmon through endocrine mechanisms.

330   *American Journal of Physiology: Regulatory, Integrative and Comparative*

331   *Physiology* **278**, 1352-1361.

332 Nordgarden U., Oppedal F., Hansen T. & Hemre G.I. (2003) Seasonally changing

333   metabolism in Atlantic salmon (*Salmo salar* L.) I – growth and feed conversion.

334   *Aquaculture Nutrition* **9**, 287-293.

335 Oppedal F., Taranger G.L., Juell J.-E., Fosseidengen J.E. & Hansen T. (1997) Light

336   intensity affects growth and sexual maturation of Atlantic salmon (*Salmo salar*)

337   postsmolts in sea cages. *Aquatic Living Resources* **10**, 351-357.

338 Oppedal F., Taranger G.L., Juell J.-E. & Hansen T. (1999). Growth, osmoregulation and

339   sexual maturation of underyearling Atlantic salmon smolt *salmo salar* L. exposed to

340   different intensities of continuous light. *Aquaculture Research* **30**, 491-499.

341 Oppedal, F., Berg, A., Olsen, R.E., Taranger, G.L., & Hansen, T., 2006. Photoperiod in

342   seawater influence seasonal growth and chemical composition in autumn sea-

343   transferred Atlantic salmon (Salmo salar L.) given two vaccines. *Aquaculture*. **254**,

344   396-410.

345 Pierce A.L., Beckman B.R., Shearer K.D., Larsen D.A. & Dickhoff W.W. (2001) Effects of

346   ration on somatotropic hormones and growth in coho salmon. *Comparative*

347   *Biochemistry and Physiology B* **128**, 255-264.

348 Saunders R.L., Henderson E.B. & Harmon P.R. (1985) Effects of photoperiod on juvenile

349   growth and smolting of Atlantic salmon and subsequent survival and growth in sea

350   cages. *Aquaculture* **45**, 55-66.

351   Saunders R.L., Specker J.L. & Komourdjian M.P. (1989) Effects of photoperiod on growth

352   and smolting in juvenile Atlantic salmon (*Salmo salar*). *Aquaculture* **82**, 103-117.

353   Skilbrei O.T., Hansen T & Stefansson, S.O. (1997) Effects of decreases in photoperiod on

354   growth and bimodality in Atlantic salmon *Salmo salar* L. *Aquaculture Research* **28**,

355   43-49.

356   Solbakken V.A., Hansen T. & Stefansson S.O. (1994) Effects of photoperiod and

357   temperature on growth and parr-smolt transformation in Atlantic salmon (*Salmo*

358   *salar* L.) and subsequent performance in seawater. *Aquaculture* **121**, 13-27.

359   Stefansson S.O., Naevdal G. & Hansen T. (1989) The influence of three unchanging

360   photoperiods on growth and parr-smolt transformation in Atlantic salmon, *Salmo*

361   *salar*. *Journal of Fish Biology* **35**, 237-247.

362   Taranger G.L., Haux C., Hansen T., Stefansson S.O., Bjornsson B.T., Walther B.T. &

363   Kryvi H. (1999). Mechanisms underlying photoperiodic effects on age at sexual

364   maturity in Atlantic salmon, *salmo salar*. *Aquaculture* **177**, 47-60.

365   Taylor J.F., Migaud H., Porter M.J.R. & Bromage N.R. (2005) Photoperiod influences

366   growth rate and plasma insulin-like growth factor-I levels in juvenile rainbow trout,

367   *Oncorhynchus mykiss*. *General and Comparative Endocrinology* **142**, 169-185.

368   Taylor J.F., North B.P., Porter M.J.R., Bromage N.R. & Migaud H. (2006) Photoperiod can

369   be used to enhance growth and improve feeding efficiency in farmed rainbow trout,

370   Oncorhynchus mykiss. *Aquaculture* **256**, 216-234. 2006.

371   Thorpe J.E., Adams C.E., Miles M.S. & Keay D.S. (1989) Some influences of photoperiod

372   and temperature on opportunity for growth in Juvenile Atlantic salmon, *Salmo salar*

373   L. *Aquaculture* **82**, 119-126.

374   Villarreal C.A., Thorpe J.E. & Miles M.S. (1988) Influence of photoperiod on growth

375   changes in juvenile Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology* **33**,

376   15-30.

377

378 **Figure Legends**

379 **Figure 1.** The timing of experimental LL regimes in relation to ambient water temperature
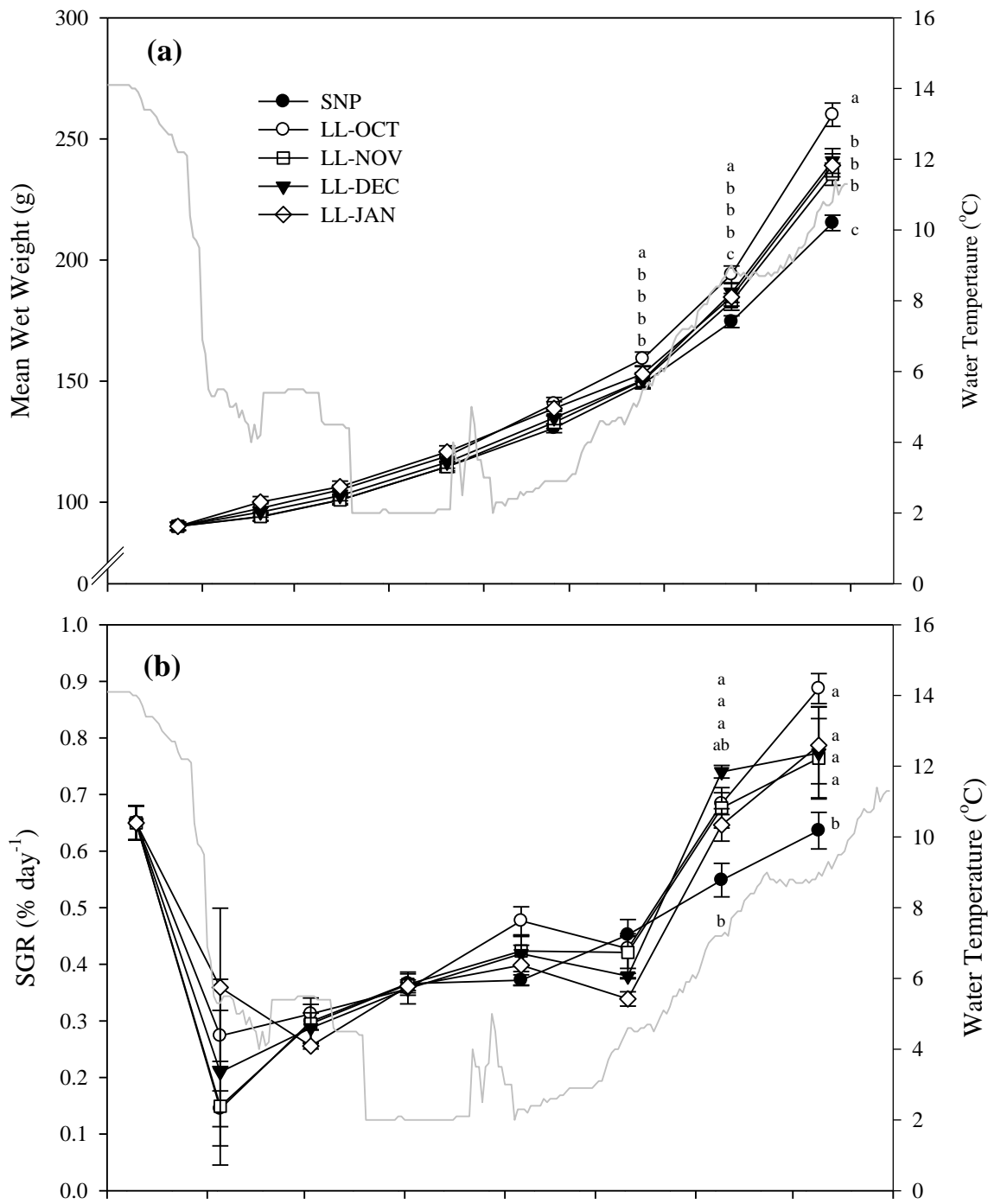
380 (Grey line) and photoperiod.

381

382 **Figure 2. (a)** Weight gain (g) and **(b)** weight specific growth rate (% day^{-1}) **(c)** condition

383 factor (K) of rainbow trout exposed to LL from October, November, December or January

384 relative to those maintained under SNP. Data are presented as tank mean ± SEM (n=3, 50

385 fish/tank). Superscripts denote significant differences between treatments (p<0.05). The

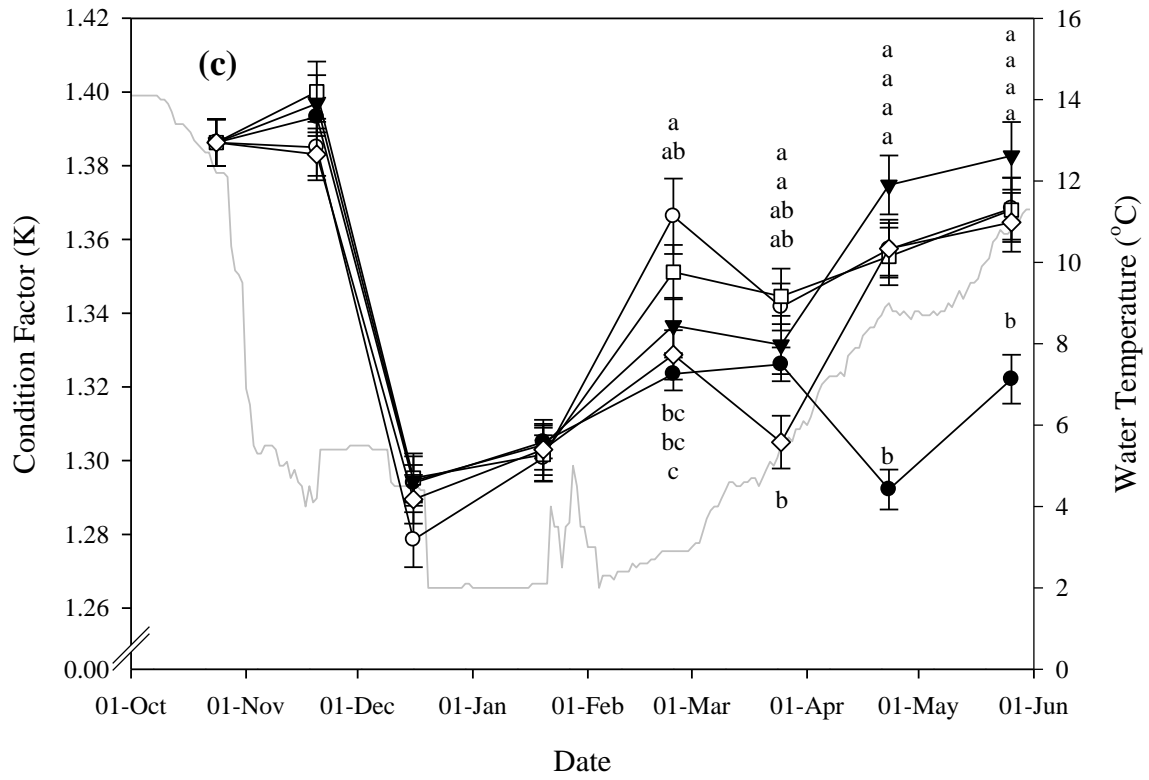386 grey line represents ambient water temperatures (ºC).

387
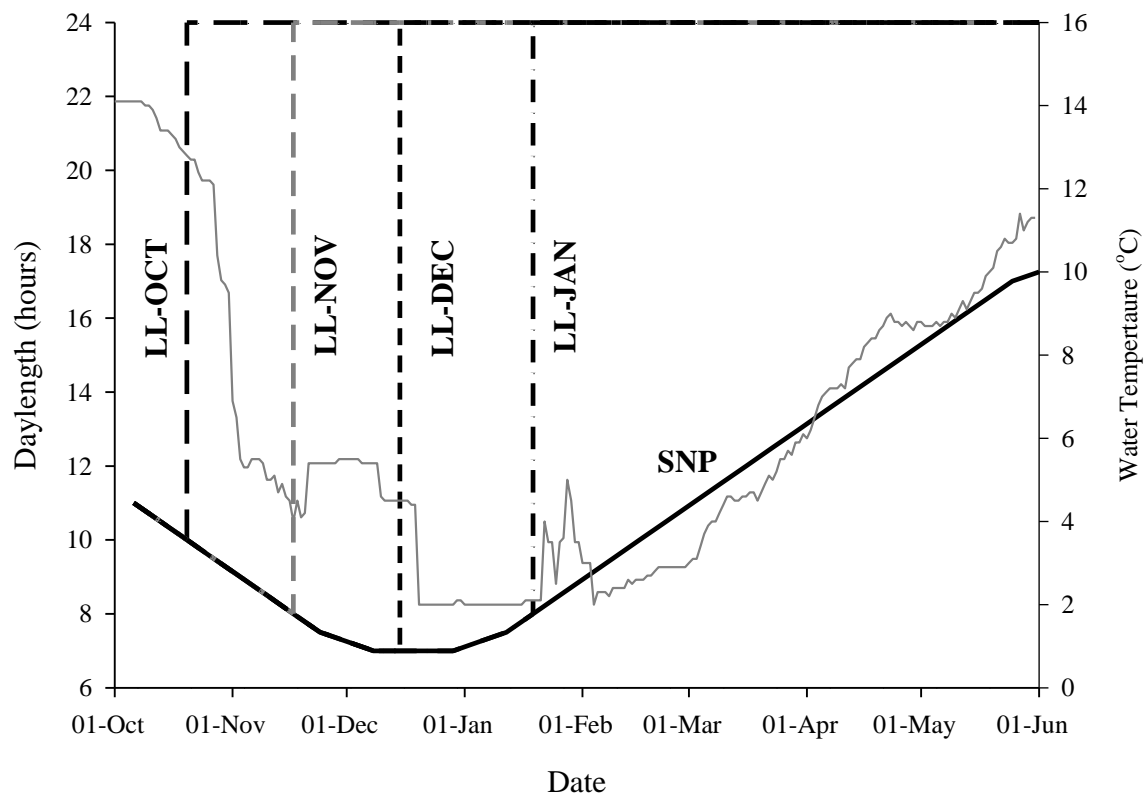
388
389 **Figure 1.**
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394   **Figure 2.**

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