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**

15

16   **Abstract**

17   Photoperiod enhancement of growth is becoming an area of increasing interest as a

18   means of enhancing rainbow trout production efficiency in commercial practice. This paper

19   examines the possible implications of shortening periods of constant light (LL) exposure on

20   rainbow trout growth during autumn-spring grow out under ambient water temperatures in

21   freshwater to portion size. Triplicate groups of juvenile all-female rainbow trout were

22   permanently exposed to LL in October, November, December or January. Growth was

23   monitored and compared to those maintained under a simulated natural photoperiod (SNP)

24   until the following May. Permanent exposure to LL (all treatments) resulted in significantly

25   greater weight gain of rainbow trout than those under SNP. Furthermore, greatest growth

26   was achieved when fish were left permanently exposed to LL from October. These findings

27   suggest there may be implications for fish farmers if the period of photoperiod exposure is

28   reduced, or timing of application is not considered with regards to ambient water

29   temperatures.

30

31   **Introduction**

32   Previous trials have demonstrated that exposure of juvenile rainbow trout

33   (*Oncorhynchus mykiss*) to periods of constant light (LL) or long-days can significantly

34   improve growth rates relative to those maintained under ambient conditions (Mason,

35   Gallant, & Wood, 1991; Makinen & Ruhonen, 1992; Taylor, North, Porter, Bromage, &

36   Migaud, 2006). However, the duration of LL and the actual timing of exposure to LL has

37   not yet been determined in relation to optimising growth enhancement during autumn-

38   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

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: $K = (WL^{-3}) \times 100$. 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**,
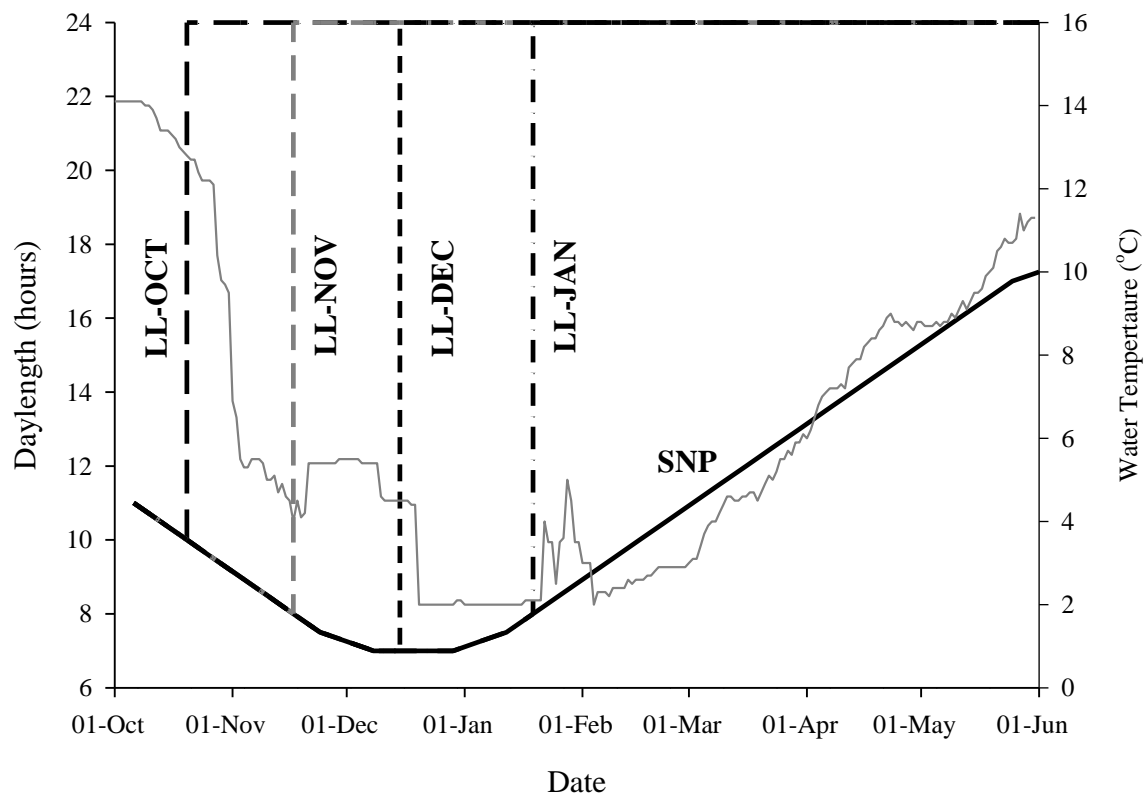
376   15-30.

377

378 **Figure Legends**

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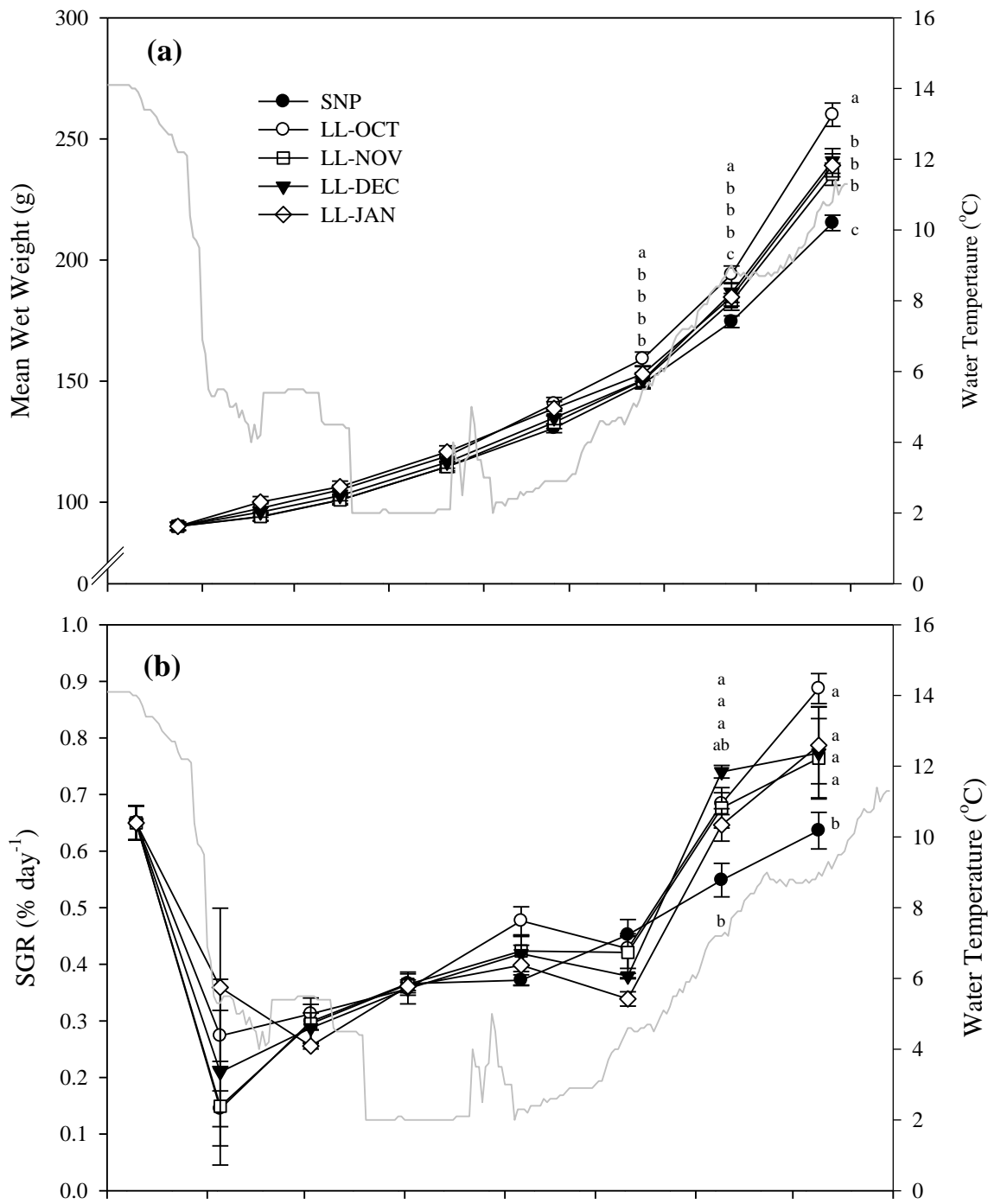
380 (Grey line) and photoperiod.

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.**
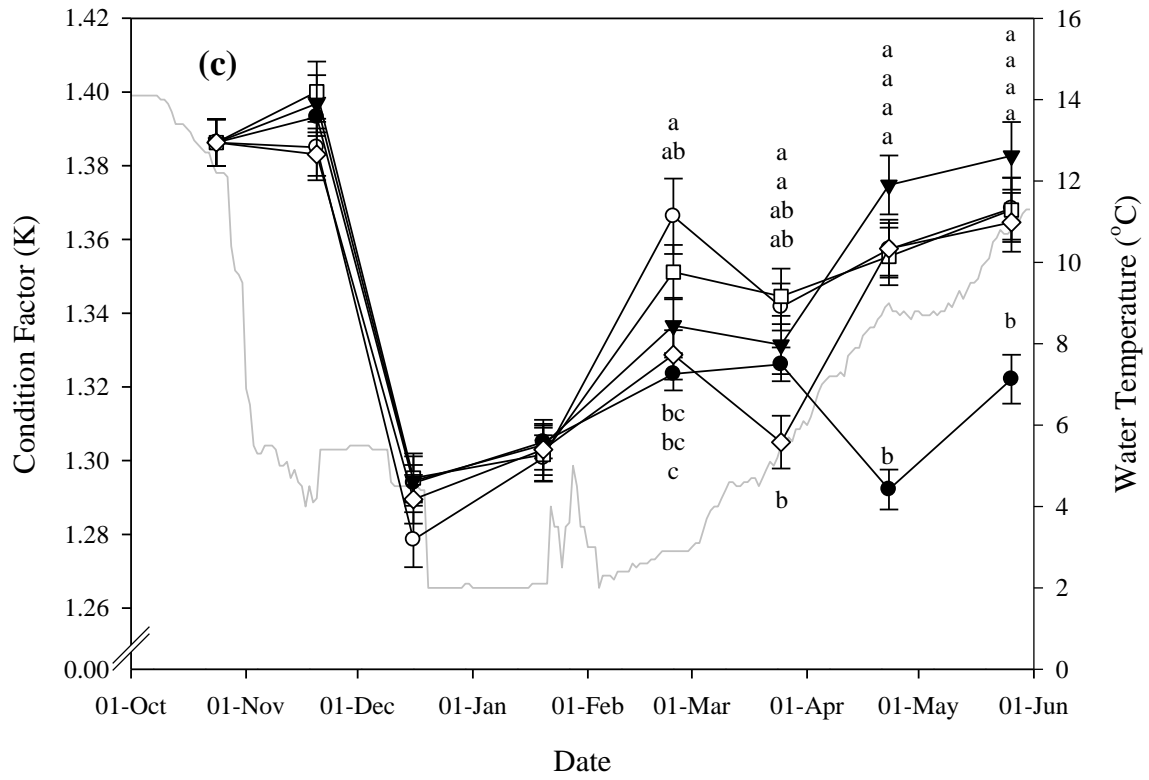390

20

(a)

Mean Wet Weight (g) / Water Temperaure (°C)

Legend:
- SNP
- LL-OCT
- LL-NOV
- LL-DEC
- LL-JAN

(b)

SGR (% day^{-1}) / Water Temperature (°C)

391
392

393
394 **Figure 2.**
395
396

397

398