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Suppression of maturation in 2-year-old Chinook salmon (*Oncorhynchus tshawytscha*) reared under continuous photoperiod

M.J. Unwin[a,*], D.K. Rowe[b], C.W. Poortenaar[c], N.C. Boustead[a]

[a]*National Institute of Water and Atmospheric Research Limited, P.O. Box 8602, Christchurch, New Zealand*
[b]*National Institute of Water and Atmospheric Research Limited, P.O. Box 11 115, Hamilton, New Zealand*
[c]*GHD PTY Ltd., GPO Box 667, Hobart 7001, Australia*

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Abstract

We investigated the effect of 24-h photoperiod (LD24:0) on the incidence of sexual maturation in freshwater-reared, 2-year-old Chinook salmon by supplying artificial lighting throughout the second year of life, from 1 May (austral autumn) to 10 April the following year. Our study populations comprised one group of monosex females, on which most New Zealand salmon aquaculture is based, and one group of mixed-sex fish. Maturation was completely suppressed in both groups of females under LD24:0, but averaged 25% and 3.6% in monosex and mixed sex female controls, respectively. Maturation was also strongly suppressed in males, being at most 7% (including some individuals which may have previously matured as yearlings) under LD24:0 compared to 90% in the controls. At age 2, mature females were longer and heavier than immature females, but after adjusting for differences between mature and immature fish neither mean fork length, total weight, nor somatic weight differed between the LD24:0 and control groups. Fish subjected to LD24:0 tended to have higher condition factors than the controls, particularly from spring to early summer. Our results contrast with an earlier study in which LD24:0 initiated on 30 August (austral late winter) had no effect on the incidence of maturation in 2-year-old Chinook females, suggesting that the onset of maturation is linked to seasonal photoperiod signals during autumn and winter.

Keywords: Chinook salmon; *Oncorhynchus tshawytscha*; Maturation; Continuous photoperiod

1. Introduction

In recent years, use of photoperiod manipulation as a tool for managing and controlling sexual maturation in the salmonid aquaculture industry has developed rapidly. Research over the last two decades has clearly established that seasonal changes in day length provide the cues which trigger the initiation of maturation in many teleosts, including salmonids (reviewed by Bromage et al., 2001). Such studies have demonstrated that artificial manipulation of photoperiod can be used either to alter the seasonal timing of maturation (e.g.,

* Corresponding author. Tel.: +64 3 348 8907; fax: +64 3 348 5548.
E-mail address: m.unwin@niwa.co.nz (M.J. Unwin).

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Johnson, 1984; Duncan et al., 1999), or to reduce its incidence (e.g., Hansen et al., 1992; Taranger et al., 1998; Porter et al., 1999). For Atlantic salmon (*Salmo salar*), the most widely cultured and best studied of the salmonids, there is general agreement that the incidence of grilsing can be greatly reduced by subjecting fish to continuous photoperiod during the year before maturation is expected to be completed, although the timing and duration of this treatment have been variable. Commencement dates have ranged from midautumn (within a few weeks of the autumnal equinox) to the winter solstice, and treatment duration from less than 6 months to 12 months or more (e.g., Hansen et al., 1992; Oppedal et al., 1997; Porter et al., 1999; Kadri, 2003).

In New Zealand, commercial salmon aquaculture is based solely on Chinook salmon (*Oncorhynchus tshawytscha*), which were introduced (from the Sacramento River, California) in the 1900s (McDowall, 1994) and have been farmed since ca. 1980 (McDowall, 1990). On most farms the problems associated with early maturation have been circumvented primarily by using monosex female stocks (e.g., Brannon, 1991; Willoughby, 1999). Female Chinook salmon typically mature at least 1 year later than males, and, within their native range, seldom if ever mature before the end of their third year of life (Healey, 1991). However, maturation at age 2 has been consistently observed in a small proportion (1.2–4.7%) of Chinook females in many anadromous New Zealand populations (Quinn and Unwin, 1993), and has become increasingly common in cultured stocks as husbandry practices and growth rates improve (Unwin et al., 2004), causing production losses as high as 20% for some farms. There is thus considerable potential for using photoperiod manipulation to suppress maturation, particularly in 2-year-old females.

The primary aim of this study was to determine the effect of a continuous 24 h photoperiod, during the second year of life, on the incidence of maturation in 2-year-old Chinook salmon. Although a previous study focussed solely on females (Unwin et al., 2004), the present study included a mixed sex group as well as a monosex female group, so as to explore maturation rates in both sexes. A secondary aim was to determine the effects of exposure to continuous light on growth and condition during the second year of life.

2. Methods

2.1. Rearing protocols

Fish for this study were obtained from yearling production stock reared at the National Institute of Water and Atmospheric Research's (NIWA) Silverstream Research Station (43°25′S, 172°35′E). Monosex females were sourced from 3-year-old captive female broodstock, using milt from 2-year-old phenotypic male, genotypic female broodstock (e.g., Donaldson and Devlin, 1996), over a 16-day period from 26 April to 12 May 2001. Mixed sex fish were sourced from sea-run Chinook released from Silverstream in 1997 and 1998 which returned to the hatchery as 3- and 4-year-olds, and were spawned on 11 and 15 May. All fish hatched 35 days after stripping.

On 1 May 2002 (austral mid-autumn, 361–380 days post-fertilisation), we established a pooled study population of monosex females (mean weight 134 g) and mixed-sex fish (mean weight 68 g) by randomly assigning approximately 200 monosex and 400 mixed-sex individuals (numbers being estimated by bulk weighing) to each of four circular ponds, 6 m in diameter×0.8 m deep, supplied with ambient groundwater (mean temperature 11–14 °C). Monosex fish were marked externally by excision of the adipose fin. Fish were hand-fed three times daily with a commercial salmon diet (Reliance Stockfoods, Dunedin), increasing the feeding rate as necessary to ensure fish were fed to satiation while maintaining the same delivery rate (kg/day) across all ponds. Further details of standard husbandry practices at Silverstream, including incubation and rearing protocols during the first year of life, are given by Kinnison et al. (1998).

From 1 May 2002 to 10 April 2003 we provided additional lighting to two ponds using centrally located Pisces-5 underwater cage illuminators (Aquabeam, England) which were switched on during the hours of darkness (1 h before sunset to 1 h after sunrise), providing a minimum illumination of 300 lux at the perimeter of each pond. A light-proof black plastic screen was installed between the lit and unlit ponds to prevent stray illumination of the unlit ponds. Thus, the experiment consisted of three distinct treatment groups (monosex females, mixed-

sex females, and mixed-sex males), all of which were exposed to ambient daylight during the light phase, and either natural lighting (LDN) or continuous 24 h lighting (LD 24:0) during the dark phase. Our choice of a 1 May starting date for the LD24:0 treatment was guided by an earlier study which established that macroscopic ovarian development in post-yearling female Chinook began in mid September, and may have been associated with transient increases in plasma 17β-estradiol and testosterone during August (Unwin et al., 2004). Exposure to LD24:0 from late August in this study had no effect on the incidence of maturation; consequently, we advanced the start of the treatment by 4 months so as to be sure of preceding any August physiological switch.

2.2. Data collection

On 29 April 2002 (i.e., 1 day before they were assigned to the circular ponds), we collected random samples of 30 monosex and 60 mixed-sex fish to provide baseline data for the whole study population. Thereafter, we sampled each pond every 4–6 weeks from 3 July 2002 to 8 April 2003, to obtain 10 samples over 40 weeks at ages ranging from 14 to 23 months. Each sample included 10 monosex females and 30 mixed-sex fish, the latter yielding an average of 17 females (range 12–21) and 13 males (range 9–18) per sample. Fish were sacrificed by administering a lethal dose of 2-phenoxyethanol, and fork length (FL, mm), total body weight (W, to 0.1 g), sex, and gonad weight (W_{gonad} to 0.001 g) recorded for each fish. The experiment was terminated on 10 April 2003, 2 days after the final sample was taken, at which time we recorded FL, W, and W_{gonad} for all remaining fish. These data were pooled with those collected 2 days earlier so as to measure the proportion of maturing fish for each treatment and pond. Somatic weight ($W_{som}=W-W_{gonad}$), condition factor ($CF=10^5\times W/FL^3$), and gonadosomatic index ($GSI=100\times W_{gonad}/W$) were calculated for all fish. Fish were classified as either maturing or immature depending on GSI, taking into account any tendency towards bimodality, using a threshold of 0.4% for females in all months except April 2003 (when we increased the threshold to 1%; see Unwin et al., 2004), and 0.2% for males.

2.3. Data analysis

Maturation rates for each sex and treatment group were estimated directly from the counts of mature and immature fish recorded on 8–10 April 2003, using confidence intervals based on the binomial distribution to assess the significance of differences between treatments. To characterise variation in body size (FL, W, and W_{som}, log-transformed as necessary to normalise distributions) and condition factor between treatments at the end of the study (i.e., April 2003), relative to maturation status, we used ANOVA with treatment and maturation status (S) as fixed effects, a treatment$\times S$ interaction (for groups which generated no empty cells), and ponds nested within treatment. We analysed data for each experimental group separately because preliminary ANOVA of pooled data for all three groups showed significant third and higher order interaction terms involving sexes and groups, detailed analysis of which was secondary to our main objective. We used the same model to analyse seasonal trends in body size and condition factor during the 10-month study period, deleting terms involving S as appropriate for samples which included no maturing fish.

Preliminary analysis suggested that the probability of an individual fish maturing tended to increase with body size, as expected, but that differences in maturation rates between the two female groups could not be accounted for solely by size. To clarify this result, we used logistic regression (Steinberg and Colla, 2000) to characterise variation in S (coded as a binary variable) with FL, including an additional categorical variable to distinguish between the monosex and mixed sex groups, and an interaction between group and FL. In the event (see Results) we found no maturing females in the LD24:0 ponds, so this analysis was restricted to females from the two LDN control ponds measured in April 2003 (pooled across ponds because of the small number of mature fish in the mixed sex group). The model used was thus:

$$logit(S_{ij}) = \mu + FL_i + \mathrm{Group}_j + FL_i \times \mathrm{Group}_j + \varepsilon_{jk},$$

analogous to a conventional ANCOVA with covariate FL and two levels of Group.

All statistical tests were conducted at a significance level of 95%. Confidence intervals for means (back-

transformed as necessary) are presented as ±2 standard errors unless otherwise stated. All calculations were performed using the GLM and Logistic Regression modules in SYSTAT® 10 (Wilkinson, 2000).

3. Results

3.1. Maturation rate

Suppression of maturation in female Chinook salmon under the LD24:0 treatment was complete in both the monosex and mixed sex groups. For monosex females, the maturation rate averaged 25.0±5.8% (55 of 220 fish) in the LDN controls compared to zero (0 of 270 fish) in the LD24:0 ponds (Table 1). A maturation rate of zero was also recorded in the mixed sex females, although the rate was only slightly higher (3.6±3.1%) in the LDN controls. With the possible exception of four fish with slightly enlarged gonads (0.44%≤GSI≤0.53%) recorded in December 2002 and January 2003, all from the monosex group, we found no maturing fish among 602 females from the LD24:0 ponds examined over the final 20 weeks of the study (19 November 2002 to 10 April 2003), during which time the distribution of GSIs in the LDN controls was unambiguously bimodal (Fig. 1).

Maturation was also strongly suppressed in males subjected to the LD24:0 treatment, falling from 89.9±5.5% in the controls to 6.8±5.0% in the treatment ponds (Table 1). However, this result was slightly confounded by the presence of mature yearling parr in the initial sample collected on 29 April 2002 (2 out of 34 fish), and in all but one of the subsequent samples (Fig. 1). These fish, all with GSIs of at least 4%, were last recorded in the LDN group on 27 August 2002, but made up 6.1% (14 out of 229) fish examined in the LD24:0 group between 3 July 2002 and 11 March 2003. The LD24:0 treatment was notable also for the absence of males with GSIs between 0.2% and 4%. In contrast to the LDN treatment, where a steady increase in GSI throughout the study period was consistent with normal gonad development, males from the LD24:0 group showed no evidence of any intermediate developmental stage (Fig. 1). It is possible, therefore, that some (and perhaps all) of the seven mature males recorded in the LD24:0 group in April 2003 were maturing for the second time after first maturing as 1 year old fish in April 2002. This interpretation is supported by treatment-specific differences in the relationship between maturation status and male body size at the end of the experiment in April 2003, presented in a later section.

Mean GSIs for fish identified as maturing on 8–10 April 2003 were 17.0±0.6% for monosex females, 14.1±2.3% for mixed sex females, and 8.8±0.3% for males. The corresponding figures for immature fish were 0.26±0.01%, 0.22±0.01%, and 0.08±0.01%, respectively.

Table 1
Incidence of sexual maturation in three groups of 2-year-old Chinook salmon reared under natural photoperiod (LDN) and continuous 24 h lighting (LD24:0) during their second year of life

Group	Replicate	LDN (controls)			LD24:0 (treatment)		
		N	N_{mat}	% mature	N	N_{mat}	% mature
Female (monosex) (902±21 g)	1	101	23	22.8±8.3	152	0	0
	2	119	32	26.8±8.1	127	0	0
	Total	220	55	25.0±5.8	279	0	0
Female (mixed sex) (761±28 g)	1	79	2	2.5±3.6	56	0	0
	2	58	3	5.2±5.8	53	0	0
	Total	137	5	3.6±3.1	109	0	0
Male (mixed sex) (867±45 g)	1	59	53	89.8±8.0	49	6	12.2±9.5
	2	60	54	90.0±7.8	54	1	1.9±3.7
	Total	119	107	89.9±5.5	103	7	6.8±5.0

For each experimental group, treatment, and replicate, the table shows the total number of fish examined on 8–10 April 2003 (N); the number of fish identified as maturing (N_{mat}); and the percentage maturation rate (±95% confidence interval). Mean weights for each group (±95% confidence interval), averaged over all fish, are shown in parentheses.

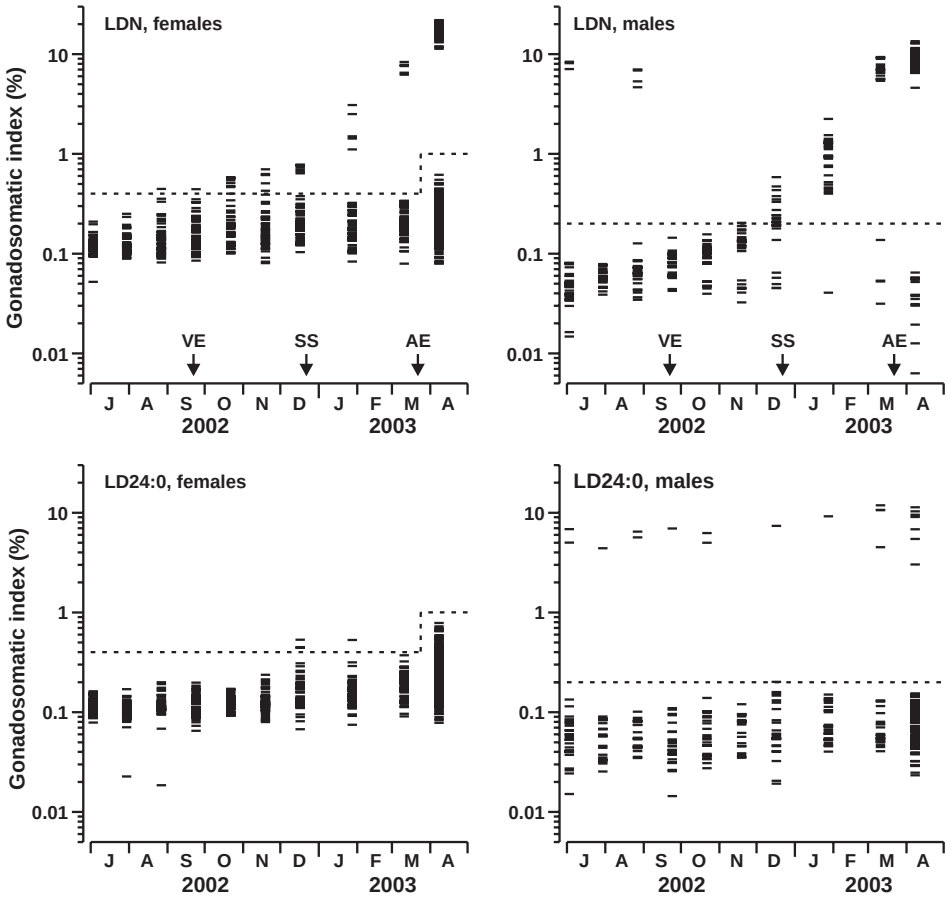

Fig. 1. Variation in gonadosomatic index with sampling date, July 2002 to April 2003, for female and male Chinook salmon reared under natural photoperiod (LDN) and continuous 24 h lighting (LD24:0) during their second year of life. The southern hemisphere vernal equinox (VE), summer solstice (SS), and autumnal equinox (AE) are arrowed. Data for monosex and mixed-sex females are pooled, and the nominal cut-off between immature and maturing fish, for each sex, is indicated by the dashed line. Note that the *y*-axis is logarithmic.

3.2. Size, growth, and condition

The LD24:0 treatment had no direct effect on body size at age 2 (April 2003) for all three groups of fish, in terms of either fork length ($p \geq 0.27$), total weight, or somatic weight ($p \geq 0.22$; Table 2). However, fish exposed to LD24:0 tended to have slightly higher condition factors than the LDN controls, the effect being strongest ($p = 0.001$) in monosex females, and weakest ($p = 0.05$) in males (Table 2, Fig. 2). Growth profiles for each group over the duration of the study conformed to a similar pattern. Fork length, total weight (Fig. 2), and somatic weight (not shown) generally differed little if at all between treatments, apart from a few exceptions (e.g., males from the 26 August sample) which we interpret as isolated results (possibly reflecting small sample sizes) rather than indicative of a general trend. By contrast, differences in condition factor were consistent across all three groups, particularly from late August to December (spring to early summer), when fish exposed to LD24:0 tended to have higher CFs than the controls.

With one exception, no significant pond effects were evident in any of the preceding analyses. The exception occurred in the final samples collected on 8–10 April 2003, for which females in one of the LD24:0 replicates had anomalously high CFs compared to those in the other three ponds ($p < 0.001$).

Table 2
Significance tests (F-statistics and associated p values) for four measures of growth and condition, as influenced by photoperiod treatment, maturation status, and replicate (nested within treatment), for three groups of 2-year-old Chinook salmon examined at the end of the study period in April 2003

Group	Factor (*df*)	Fork length		Total weight		Somatic weight		CF	
		F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Female (monosex) (n=499)	photoperiod (1)	1.20	0.274	0.02	0.887	0.02	0.895	*10.93*	*0.001*
	maturity (1)	*57.68*	*≪0.001*	*64.57*	*≪0.001*	*9.51*	*0.002*	*16.37*	*<0.001*
	replicate (2)	0.52	0.596	3.57	*0.029*	3.79	*0.023*	*21.13*	*≪0.001*
Female (mixed sex) (n=246)	photoperiod (1)	0.14	0.708	1.48	0.225	1.52	0.219	*7.28*	*0.007*
	maturity (1)	*7.18*	*0.008*	*6.66*	*0.010*	2.04	0.155	0.78	0.378
	replicate (2)	1.69	0.187	0.30	0.742	0.27	0.761	*3.51*	*0.032*
Male (mixed sex) (n=222)	photoperiod (1)	0.51	0.476	0.01	0.918	0.002	0.961	3.87	0.050
	maturity (1)	1.24	0.266	*7.24*	*0.008*	2.79	0.096	*39.26*	*≪0.001*
	replicate (2)	0.71	0.492	1.28	0.281	1.34	0.264	*3.60*	*0.029*
	photoperiod×maturity (1)	*31.67*	*≪0.001*	*30.64*	*≪0.001*	*29.75*	*≪0.001*	2.53	0.113

The degrees of freedom (*df*) for each factor is given in parentheses; effects significant at $p<0.05$ are italicised.

To elucidate this result for the monosex female group (which showed the strongest effect), we used ANCOVA to estimate mean weight for the fish in each pond adjusted to a common mean FL of 389 mm. Mean weights were 883±10 g (mean CF=1.50) for the anomalous pond, compared to 835±10 g, 837±10 g, and 852±10 g (1.42≤mean CF≤1.45) in the other three ponds. A similar but weaker (p=0.06) trend was apparent among males. However, we could not reject the null hypothesis that the maturation rate did not differ between ponds within treatments (females: p=0.22; males: p=0.10). We interpret these results as evidence of subtle differences between the rearing environments provided by the four ponds, which were detectable only because of the larger sample size available at the end of the experiment. Nevertheless, it appears that these were insufficient to confound our main findings regarding the effect of the LD24:0 treatment on the maturation rate for each sex.

3.3. Influence of body size on maturation rate

Maturing fish generally tended to be larger than immature fish, but the strength of this relationship varied between sexes, and (in males) was strongly confounded by treatment specific effects. For females, this tendency (based on data for the LDN controls only) was consistent across both the monosex and mixed sex groups (ANOVA model 1, $p\leq0.001$; Tables 2 and 3). Maturing females were longer and heavier than their immature counterparts, but the difference was much more apparent in terms of total body weight (i.e., including gonads) than somatic weight (excluding gonads), suggesting that it was related more to ovarian development than to somatic growth (Table 2). The general trend was well described by the logistic regression model (McFadden's rho-squared=0.317), with no evidence of a significant interaction between FL and group (p=0.80). Re-estimating the model without the interaction term confirmed a highly significant ($p\ll0.001$) tendency for the probability of maturation to increase with FL, and a weaker but still significant (p=0.028) group effect, with monosex females being more likely to mature than mixed sex females of the same length (Fig. 3). Inspection of the logistic regression parameters showed that the length at which the probability of maturation model equalled 50% was 435 mm for the monosex females, compared to 457 mm for mixed sex females.

For males, ANOVA results for all three measures of body size were dominated by a strong treatment×maturation status term, which accounted for 91%, 76%, and 85% of the explained variance in fork length, total weight, and somatic weight, respectively. Inspection of means by treatment and maturation status (Table 3) confirmed that mature males were larger than immature males in the LDN controls, in accordance with their female counterparts, but that the reverse was true in the LD24:0

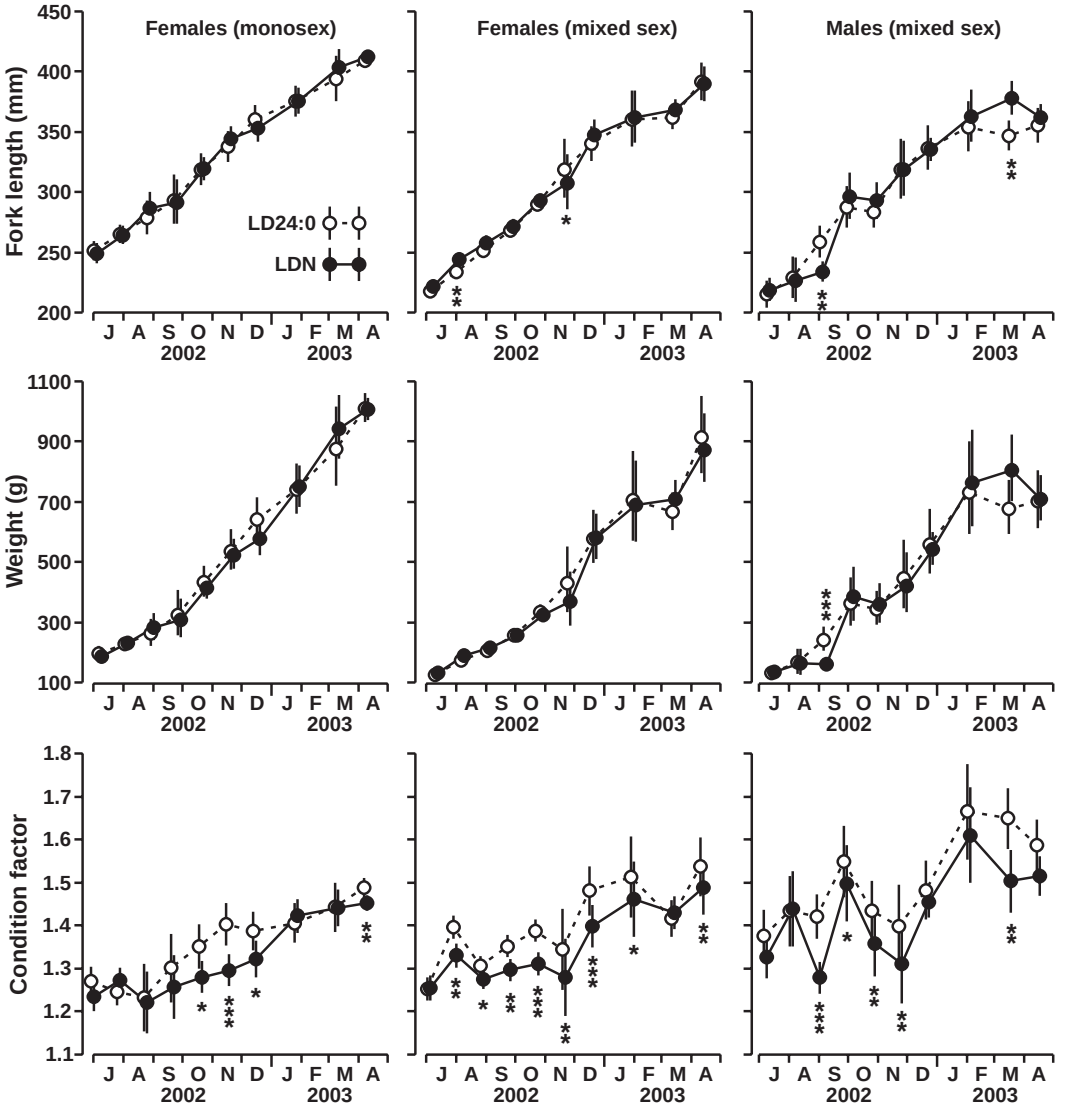

Fig. 2. Variation in mean fork length, weight, and condition factor with sampling date, July 2002 to April 2003, for female and male Chinook salmon reared under natural photoperiod (LDN) and continuous 24 h lighting (LD24:0) during their second year of life. Plots in the same row share a common vertical scale; vertical bars within each plot indicate two standard errors. Means which differ significantly between treatments after adjusting for maturation status and pond (replicate) effects are indicated by *($p<0.05$); **($p<0.01$); or ***($p<0.001$).

treatment group. We interpret this apparently anomalous result as further evidence that males recorded as maturing under the LD24:0 treatment had previously matured as yearlings in autumn 2002 and remained in a state of semi-maturity throughout the study, thereby drawing on energy reserves which would otherwise have been directed towards increased somatic growth.

4. Discussion

For 2-year-old Chinook salmon reared under continuous artificial photoperiod throughout their second year of life, suppression of maturation in females was unequivocal and complete. Our results for males were slightly less definitive, because of the likelihood that some of the mature 2-year-old

Table 3
Differences in mean fork length (FL, ±two standard errors) between immature and mature fish in April 2003, by experimental group and treatment, for the same data sets as in Table 1

Group	Treatment	Immature		Mature		Trend	*p*
		N	FL	N	FL		
Female (monosex)	LDN	165	395 ± 5	55	429 ± 6	mature > immature	<0.001
	LD24:0	279	392 ± 3	no data		–	
Female (mixed sex)	LDN	132	371 ± 5	5	410 ± 45	mature > immature	0.026
	LD24:0	109	372 ± 6	no data		–	
Male (mixed sex)	LDN	12	332 ± 27	107	395 ± 8	mature >immature	<0.001
	LD24:0	96	376 ± 7	7	338 ± 44	immature>mature	0.004

For groups which included both immature and mature individuals, the table also shows the direction of the trend in mean FL, and its significance level.

fish we identified in autumn 2003 had previously matured as yearlings in autumn 2002, but also show that maturation was strongly (and possibly completely) suppressed under LD24:0. The clarity of our experimental results, and the extent to which maturation was suppressed in both sexes, suggest that the method should be directly applicable to New Zealand's salmon aquaculture industry.

The artificial photoperiod regime we used in this study was simple, involving a single switch from natural to continuous photoperiod on 1 May 2002, approximately 6 weeks after the austral autumnal equinox and 7 weeks before the winter solstice. Continuous lighting was then maintained throughout the second year of life, until the following autumn, well after maturation was underway in most fish. Our results are consistent with other studies showing that exposure to continuous photoperiod from late autumn suppresses maturation in Atlantic salmon (Hansen et al., 1992; Oppedal et al., 1997; Taranger et al., 1998; Porter et al., 1999), although the opposite effect (i.e., increased maturation in response to LD24:0) has also been observed (e.g., Kråkenes et al., 1991; Endal et al., 2000). A more complex lighting regime, involving an abrupt shift from LD18:6 to LD8:16, was used by Duston et al. (2003) to partially suppress maturation in Arctic charr (*Salvelinus alpinus*), following earlier studies on Atlantic salmon in which continuous light had yielded mixed results (Porter et al., 1999). However, Duston et al. (2003) exposed fish to long periods of light from late winter (February) until late autumn (November), whereas our treatment began in late autumn (May), 3–4 months earlier allowing for the boreal reversal of seasons, and was highly effective in suppressing maturation. By contrast, a late winter (August) start had no effect on the incidence of maturation in 2-year-old female Chinook salmon, in a precursor to the present study in 2002 (Unwin et al., 2004). Collectively, these results clearly establish that an early start for photoperiod manipulation is important for Chinook. However, complete disruption of entrained endogenous physiological cycles through photoperiod manipulation may take some months, and the minimum duration of this manipulation has yet to be determined.

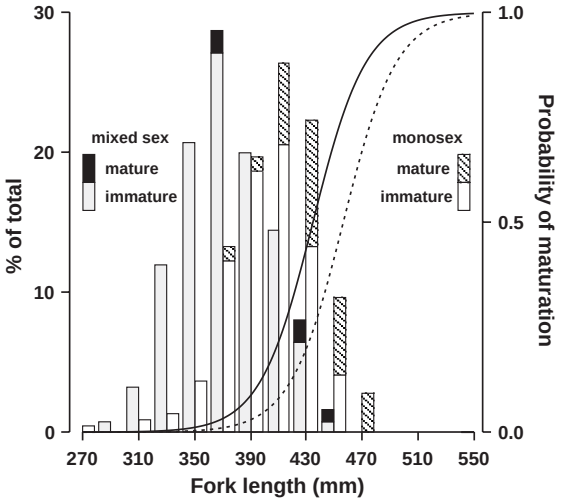

Fig. 3. Length frequency histograms for two groups of 2-year-old female Chinook salmon reared under natural photoperiod during their second year of life, 8–10 April 2003. Logistic regression curves showing the probability of maturation as a function of fork length, for monosex (solid line) and mixed sex females (dashed line), are superimposed.

From spring to early summer (September to December), both male and female fish exposed to continuous lighting tended to have higher condition factors than their LDN counterparts. These differences first occurred at a time when gonad development in the LDN controls was already underway, but well before mean gonad weights for maturing fish (as evidenced by changes in GSI) exceeded 1% of total body weight. This indicates that at this time, fish exposed to continuous lighting were accumulating somatic reserves at a faster rate than the LDN controls, and is consistent with the spring increase in condition factor in maturing salmon reported in many other studies (e.g., Hunt et al., 1982; Johnston et al., 1987; Rowe and Thorpe, 1990; Hopkins and Unwin, 1997). The differences in condition we observed between LDN and LD24:0 fish during summer and autumn months were related mainly to gonadal rather than somatic growth. This effect may have been slightly confounded by pond-specific differences in CF which were detected only at the end of the study, but the feeding regime was the same for all ponds irrespective of photoperiod treatment, so that the difference in growth rates between the two treatments was not due to increased food availability. Exposure to continuous light may have increased the efficiency of food assimilation, possibly via hormonal influences on growth (e.g., Saunders and Harmon, 1990; Stefansson et al., 1991). Even though GSIs in maturing fish were only slightly elevated at this time, the energetic costs associated with the onset of maturation may have been sufficient to effect a concomitant reduction in growth. Differences in CF were less pronounced over the final four months of the study, from January to April 2003, but are consistent with an energetic trade-off between reproductive development and somatic growth.

The 25% maturation rate we observed in the larger of the two groups of 2-year-old female Chinook salmon in this study is almost four times higher than the figure of 6.9% we have reported in a previous study (Unwin et al., 2004), and up to 20 times higher than the 1.2–4.7% maturation rate which has been previously reported for anadromous New Zealand stocks (Quinn and Unwin, 1993). Such a high maturation rate is all the more remarkable given that the study fish were reared in fresh water throughout their life, under a sampling regime involving repeated handling at 4–6 week intervals—conditions which not normally be conducive to the energetically demanding process of maturation. They were also substantially smaller than their naturally produced anadromous counterparts. Sexually mature 2-year-old females in anadromous New Zealand stocks average 560–630 mm (Quinn and Unwin, 1993), whereas mature females in this study averaged 410–430 mm, with some individuals as small as 375 mm (700–800 g) and none larger than 480 mm. On the other hand, our results were consistent the general tendency for the rate of maturation to increase with body size (Thorpe, 1986), indicating that this tendency persisted in both experimental groups of females despite their relatively small size. We conclude that although rapid growth during the second winter of life favours the onset of maturation in female Chinook, other influences (which our study did not control for) are also involved. This conclusion is reinforced by the different maturation rates we observed in monosex and mixed sex females of the same length, which clearly reflects some inherent difference (which could include genetic as well as environmental factors) between these two groups. One obvious environmental factor, i.e., their initial difference in mean weight at the start of the experiment, reflects differences in husbandry during the first year of life. The monosex females were derived from fish otherwise destined for supply to various commercial salmon farms, and had been grown comparatively rapidly during their first year. By contrast, the mixed sex fish were from a group set aside for enhancement of the local sports fishery, and had deliberately been grown relatively slowly from 6 to 12 months of age. It is possible, therefore, that the developmental trajectory leading to maturation at the end of the second year of life began before the end of the first year, perhaps as early as 6–12 months after hatching.

The possibility that some males in the LD24:0 ponds which were recorded as maturing in April 2003 had previously matured as 1 year old parr is consistent with previous findings for New Zealand Chinook salmon. Although Chinook salmon are normally semelparous in the wild, iteroparity can occur under hatchery conditions, with some mature parr surviving for up to two more seasons and producing viable milt each year (Unwin et al.,

1999). The extent to which the gonads of iteroparous males are resorbed each year is unclear, although the limited data available invite the hypothesis that in at least some such individuals the gonads remain viable throughout the second (and any subsequent) years of life (Unwin et al., 1999). Our results, indicating that males with GSIs of at least 4% were present in all but one of the LD24:0 samples, are consistent with this hypothesis. However, this raises the question of why no such fish were observed in the LDN controls over the 6 months from September 2002 to February 2003. Assuming that this was not merely an artefact of the small sample size, one possibility is that the same physiological processes which were responsible for suppressing maturation in the LD24:0 males also suppressed (or tended to suppress) the reverse effect, i.e. resorbtion of gonads in mature post-yearlings. It is possible that, in the absence of any constraints on their natural endogenous cycle, LD24:0 males were able to move towards maturity at any time during the season, although the absence of intermediate GSIs (between 0.2% and 4%) suggests this is unlikely.

Numerous studies have indicated that maturation in salmonids can be suppressed if feeding, growth and acquisition of lipid reserves are reduced during a critical time of the year (e.g., Rowe and Thorpe, 1990; Rowe et al., 1991; Silverstein et al., 1998; Taranger et al., 1999; Shearer and Swanson, 2000). Photoperiod manipulation studies (e.g., Duston and Bromage, 1988; Porter et al., 1999; Taranger et al., 1999; Duston et al., 2003) suggest that this critical time of year is set by seasonal changes in day length, and can be shifted by artificially masking or disrupting these changes. The almost complete suppression of maturation in Chinook salmon in this study, compared to the absence of any such effect when the LD24:0 treatment did not begin until 30 August (Unwin et al., 2004), suggests that the critical period for this species lies within (or includes) a 4-month window from 1 May (austral mid-autumn) to 30 August (austral late winter). These results provide further support for the hypothetical model of maturation proposed by Rowe et al. (1991), in which fish "sense" whether to mature by physiologically testing the size of somatic reserves during a critical seasonal window, determined by photoperiod. It seems likely that photoperiod induced changes in melatonin levels may influence the timing of the physiological maturation switch, and so may provide a chemical analogue for photoperiod manipulation. However, the interactions between the hormonal mechanisms regulating the timing of internal physiological changes, and those responsible for initiating gametogenesis, have yet to be identified.

The 24-h photoperiod regime investigated in this study clearly has the potential to provide a useful tool for suppressing maturation of 2-year-old female Chinook in the New Zealand aquaculture industry. Moreover, our results suggest that a similar result may be possible for males, and hence that there may be some potential for reducing the current dependence on monosex female stocks, and also that the treatment can be applied to both sexes without impacting on growth rates. However, an important caveat is that the fish in our study grew more slowly, and hence were much smaller at age-2, than their equivalents on New Zealand salmon farms, reflecting the increased frequency of handling in our experimental set up compared to a dedicated production facility. Typical harvest weights at ages of 18 months to 2 years are about 1.5–1.7 kg for freshwater farms and 3–5 kg for marine farms, compared to less than 1 kg in our study, so that–given the positive correlation between maturation rate and growth rate–it does not necessarily follow that complete suppression of maturation could be expected under LD24:0 in a commercial environment. In addition, further studies are required to better define the optimal seasonal window associated with this treatment, and (more fundamentally) to identify the underlying hormonal and metabolic changes which are ultimately responsible for maturation.

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