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Effects of photoperiod and exercise on growth, liver size, and age at puberty in farmed Atlantic cod (*Gadus morhua* L.)

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Sexual maturation in Atlantic cod (*Gadus morhua*) results in loss of appetite and weight during spawning, leads to increased production time required to reach desired harvest size, and results in greater mortality and reduced food conversion efficiency. Thus, methods to stop or delay maturation are urgently needed. In the present study, the effect of continuous light (LL) treatment on maturation was tested in combination with different exercise levels in seawater tanks compared with controls under natural light. LL treatment in light-proof tanks arrested gonadal development for at least 8 months. Exercising Atlantic cod by forcing them to swim with 0, 0.5, or 1 body length per second from the summer solstice had no effect on incidence of maturation either under natural light or under LL. Growth was enhanced in the LL groups compared with the NL groups, mainly as a result of the weight loss of the NL groups during spawning.

Keywords: Atlantic cod, exercise, gonad development, light regime, sexual maturation.

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Introduction

In recent years, farming of Atlantic cod (*Gadus morhua* L.) has become increasingly successful, and there is now a stable supply of juveniles for on-growing. However, under favourable growing conditions, farmed Atlantic cod of both sexes reach sexual maturity or puberty and spawn at 2 years of age, before reaching commercial harvest size (Braaten, 1984; Godø and Moksness, 1987; Karlsen *et al.*, 1995). This may be independent of strain, as both coastal cod from western Norway and cod from the Barents Sea display close to 100% maturation at 2 years of age when reared under identical farming conditions from hatching (Svåsand *et al.*, 1996). In their natural environment, these stocks typically reach puberty at an age of 4–6 and 6–8 years, respectively (Godø and Moksness, 1987; Berg and Albert, 2003). Studies on ovarian development indicate that the number of eggs that may be spawned the following season is determined during summer when the oocytes reach the circumnuclear ring stage (Woodhead and Woodhead, 1965). Vitellogenesis, the process of yolk formation and incorporation in the growing oocytes, takes place from October/November until spawning (Kjesbu and Kryvi, 1989; Kjesbu *et al.*, 1991; Dahle *et al.*, 2003). For males, spermatids start appearing in November (Dahle *et al.*, 2003). Usually, males are prepared for spawning prior to females, and continue to spawn over a longer period. In western Norway, running males are frequently observed in early December, while females usually do not start spawning until late January or early February. Spent males and females are observed in late April.

In maturing cod, appetite is reduced on average more than a month prior to spawning and during the first three-quarters of the spawning period (Kjesbu *et al.*, 1991; Fordham and Trippel, 1999; Skjæraasen *et al.*, 2005). Moreover, Atlantic cod release 15–20 egg batches in one spawning season and allocate large amounts of energy to the gonads throughout the spawning period (Kjesbu *et al.*, 1996). Since energy requirements for gonad growth and spawning are mainly drawn from stored reserves in liver and muscle (Dambergs, 1964; Kjesbu *et al.*, 1991), spawning results in significant weight loss. Large well-fed female cod can lose up to 50% of its weight during one spawning season (Kjesbu *et al.*, 1992), while 30–35% weight loss is usually observed for recruit spawning farmed cod (e.g. Karlsen *et al.*, 1995). In addition, spawning in sea cages may result

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in unwanted release of fertilized eggs into the surrounding environment. Because of the negative impact of spawning, methods to delay age at puberty in gadoids is one of the key elements in achieving an economically and environmentally sustainable aquaculture production.

Early puberty in farmed cod is most likely linked to increased growth and energy deposition compared with wild stocks. Atlantic cod utilize the liver as a major lipid and energy store, and farmed cod typically have a liver that comprises ~12% of body weight (Lie *et al.*, 1988; Rosenlund *et al.*, 2004), whereas wild cod normally have liver sizes in the range of 3–8% of body weight (e.g. Du Buit, 1989; Marshall *et al.*, 1998). Growth rate and adiposity have been implicated as determining factors for the onset of puberty in fish, and models have been developed suggesting critical time windows in the season when growth rate, energy stores, and/or rate of energy acquisition must exceed genetically determined thresholds (e.g. Thorpe, 1986, 1994). Reduced feeding during winter was demonstrated to reduce early sexual maturation in Atlantic salmon (*Salmo salar*) (Thorpe *et al.*, 1990), and the size of the mesenteric lipid reserve is believed to be one of the major factors influencing maturation in salmon parr (Rowe *et al.*, 1991). In Chinook salmon (*Oncorhynchus tshawytscha*), both body size/growth rate and fat levels influence the onset of maturation in males (Silverstein *et al.*, 1998; Shearer and Swanson, 2000). Similarly, it has been postulated that the age at which sexual maturity is initiated in gadoids may depend upon lipid reserves (Eliassen and Vahl, 1982). Insufficient energy levels may even cause spawning to be postponed until the next year (Kjesbu *et al.*, 1991; Rideout and Burton, 2000), and therefore, it is likely that certain threshold energy levels exist for spawning to take place.

Attempts have been made, therefore, to delay puberty in farmed cod by periods of restricted feeding or starvation. However, even prolonged periods of restricted feeding have only limited effects on age at puberty and result in dramatically reduced growth. Consequently, restricted feeding is not considered as a way to combat the problem of early sexual maturation in farmed cod (e.g. Karlsen *et al.*, 1995).

Photoperiod manipulation is an effective means to control timing of puberty and spawning in a number of farmed fish species such as Atlantic halibut (*Hippoglossus hippoglossus*; Björnsson *et al.*, 1998; Norberg *et al.*, 2001), Atlantic salmon (Hansen *et al.*, 1992; Oppedal *et al.*, 1997; Porter *et al.*, 1999; Taranger *et al.*, 1999), brook trout (*Salvelinus fontinalis*; Holcombe *et al.*, 2000), gilthead sea bream (*Sparus aurata*; Kissil *et al.*, 2001), haddock (*Melanogrammus aeglefinus*; Martin-Robichaud and Berlinsky, 2004), sea bass (*Dicentrachus labrax*; Rodriguez *et al.*, 2001), and turbot (*Scophthalmus maximus*; Imsland *et al.*, 1997). Timing of spawning can be controlled by photoperiod treatment in Atlantic cod kept in indoor tanks (Hansen *et al.*, 2001; Norberg *et al.*, 2004; Skjæraasen *et al.*, 2005), and likewise, continuous light treatment has been indicated as being effective in arresting or delaying puberty in cod maintained in indoor tanks (Hansen *et al.*, 2001; Davie *et al.*, 2003). However, more variable results have been obtained when continuous light treatment has been applied to cod kept in sea cages under natural light (Taranger *et al.*, in press). Similarly, such variable results with continuous light treatment have been observed in Atlantic salmon kept in sea cages, indicating that other factors such as genetics, adiposity, growth rate, and/or body size, as well as other environmental factors interact with the LL treatment in determining its effect on puberty (Endal *et al.*, 2000; Taranger *et al.*, 2004).

Although restricted feeding periods have been found so far to have only limited effects on age at puberty in Atlantic cod (e.g. Lehman *et al.*, 1991; Kjesbu and Holm, 1994; Karlsen *et al.*, 1995), energy deposition and utilization may interact with photoperiod treatment, modulating the effect on age at puberty. Photoperiod treatment appears to be more effective when applied to Atlantic cod in indoor tanks than in sea cages (Taranger *et al.*, 2006). One of the main differences between sea cages and tanks is that the cod swim at a rather high velocity in circular tanks, whereas their swimming behaviour in sea cages can be more variable, and swimming activity is generally regarded as being less in sea cages than in tanks. Thus, increased swimming activity and exercise levels in tanks, which in turn may affect energy deposition and utilization in the liver, may be one reason for the differences in response to photoperiod treatment in cod observed between tanks and sea cages. Thus, the present study was set up to investigate whether exercise of cod maintained in 3 m circular seawater tanks can affect liver size and gonad development, and whether exercise can interact with photoperiod treatment on its effect on age at puberty in cod.

Material and methods

Fish material, experiments, and rearing conditions

Juvenile Atlantic cod, hatched in spring 1996, were fed first under semi-natural conditions in a large seawater pond (Parisvatnet; Blom *et al.*, 1991) and transferred to sea cages during summer 1996. Two thousand Atlantic cod were transferred to the Institute of Marine Research, Austevoll, during autumn 1996 and reared in circular seawater tanks (3 m diameter, 1 m water depth) with natural light. In March 1997, the cod were individually PIT-tagged (Trovan ID 100 Implantable Transponder, Trovan Ltd., UK) and distributed among six equally sized seawater tanks (tanks as above) with natural light and covered with shade nets giving 70% light reduction. In July 1997, the fish were randomly divided among 12 tanks. Six of the tanks were exposed to continuous light (LL) and six to natural light (NL) from July 1997 until August 1998. LL was supplied by metal halide lamps (Phillips 70 W MHW-TD), giving

total light intensities of about 5×10^{-4} W cm^{-2} just below the surface (measured by an OL754 Underwater Spectroradiometer, Optronics laboratories, USA) in similarly designed but lightproof tanks. Fish in each of these two light regimes were exposed to three different water velocities: high water current speed (HS), medium water current speed (MS), and low water current speed (LS), which corresponded to 1, 0.5 body length (BL) s^{-1}, and as low as possible maintaining an oxygen concentration above 85% in the outlet, respectively. This created six experimental groups with two replicates per treatment: NL-HS (natural light, high water speed), NL-MS (natural light, medium water speed), NL-LS (natural light, low water speed), LL-HS (continuous light, high water speed), LL-MS (continuous light, medium water speed), and LL-LS (continuous light, low water speed). In each of the centrally drained tanks, the water current was created by forcing the incoming water through vertically mounted inlet pipes (cf. Christiansen and Jobling, 1990). Water speed was measured with a float and was relatively stable in most of the tanks, with the exception of high speed resulting in turbulence around the outlet. No fish were positioned in this area. Water speed was increased every 6 weeks to compensate for length growth. The fish were fed to satiation daily with a commercially available dry feed (FK Torsk, NorAqua, Trondheim, Norway, dry matter proximate composition: 53.0% protein, 10.0% fat, and 17.7% carbohydrates, energy content: 19.5 MJ kg^{-1}). Temperature was measured daily. Water was pumped from 58-m depth, and the temperature increased from about 7°C in July 1997 to 10°C in November 1997, decreased to about 6°C in April 1998 and increased to about 9°C at the end of the experiment.

Measurements and sampling

All fish were measured (total length, mm) and weighed (g) every 4–10 weeks from July 1997 to April 1998. An additional, final sampling was made in August 1998. At each sampling, 15 individuals per tank were sacrificed, and liver, gonad, and viscera were excised and weighed to the nearest 0.1 g. Fish were starved for 2 days before sampling, which spanned 1 or 2 days. During sampling, the cod were anaesthetised using metomidate hydrochloride in aerated seawater. We estimated Fulton's condition factor $(K) = 100(\mathrm{BW} \times L^{-3})$, where BW is the total weight (g) and L is the total length (cm). Liver index (hepatosomatic index; HSI) was calculated as 100 × liver weight/total weight. Gonadosomatic index (GSI) was calculated as 100 × gonad weight/total weight.

Determination of gender and maturation

Gender and stage of maturity were determined by visual examination of gonads according to the maturity scale given by Sivertsen (1935) and West (1970). The gonads were classified as immature, maturing/running, or spent. In immature or early maturing females, the length of the ovary occupied less than half of the body cavity; ovaries were firm and coloured pink to orange. Ovaries of maturing females were larger, occupied more than half the body cavity, and were orange to dark red in colour. Females were designated as spawning when running eggs or hyaline eggs, visible through the ovary wall, were seen. Newly spent ovaries were smaller, contained residual eggs, and appeared bloodshot, with a purplish-red colour. Later, spent ovaries appeared firm, with a cloudy white appearance. The immature testes appeared as a long string-like organ without coils or lobes and a thin vas deferens. As the testes matured, the lobes and coils increased in size and, in running males, the testes were white and released milt at slight pressure. Newly spent testes were shrunken and bloodshot, often with white areas, and the vas deferens appeared wide and flattened. Spent males were separated from immature males by the wide and flattened vas deferens.

Statistics

All values relating to the fish were log-transformed before statistical analysis. GSI data were arc-sine transformed prior to analysis. Unless otherwise stated, a significance level (α-value) of 5% was applied. The Lilliefors test was used to analyse whether the frequency distribution was significantly different from a standard normal distribution. Length, weight, and condition factor were analysed using nested ANOVA where replicate tanks were nested under light and exercise, and in case of significant differences, followed by the Tukey HSD *post hoc* test. HSI were analysed using a two-way (gender and treatment) nested ANOVA where tanks were nested under treatment, and in case of significant differences, followed by the Tukey HSD *post hoc* test. GSI data did not always conform to normality even after transformation, and since the Mann–Whitney *U*-test showed that the tanks were not significantly different for either of the treatments, the tanks were pooled prior to analysis. The analyses were performed using Kruskal–Wallis ANOVA, and followed by a Mann–Whitney *U*-test if differences between treatments were found.

Results

Growth

During the experimental period, the experimental fish grew from 450 g to ca. 2300 g or 1600 g for the LL and NL groups, respectively (Figure 1). In June, August, and September 1997, there were no significant differences among treatments in weight (nested ANOVA, $p > 0.072$), while in November and January the NL groups were significantly heavier than the LL groups (nested ANOVA, $p < 0.02$). Between January and April 1998, NL groups lost weight, while the CL groups continued to grow (Figure 1), and significant weight differences were observed in February,

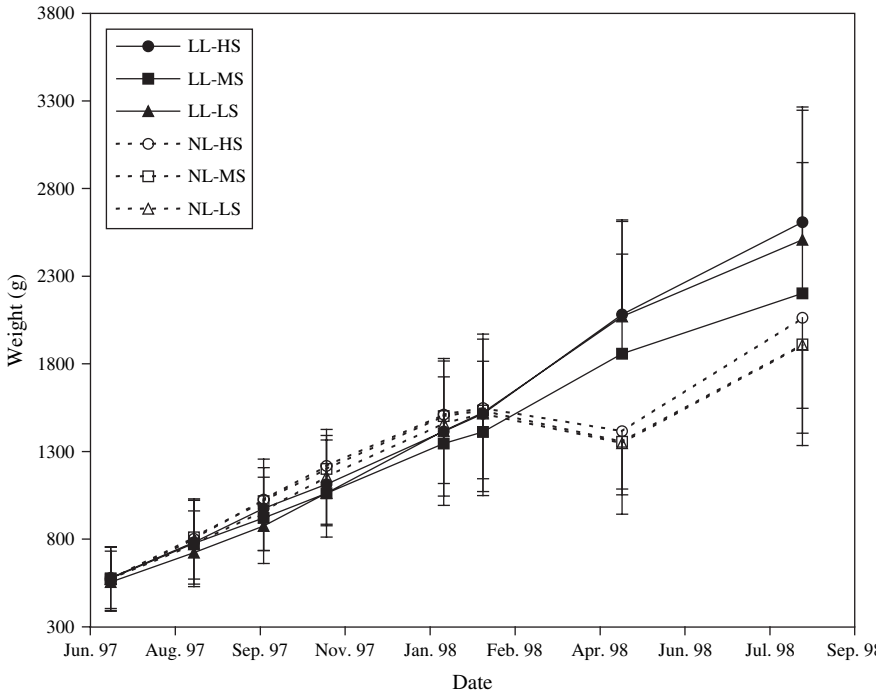

Figure 1. Total body weight (±s.d.) during the experimental period for pooled sexes exposed to natural (dotted line) and continuous (solid line) light and either high, medium, or low water current.

April, and August 1998 (nested ANOVA, $p < 0.05$). The length increased during the experimental period in the LL groups, while the length growth stagnated in the NL groups during the spawning season (Figure 2). Length was not significantly different between groups at the start or in August 1997, but in September and November 1997, the NL groups were significantly longer than the LL groups. In January 1998, there were no significant differences, but in February, April, and August 1998, the LL groups were significantly longer than the NL groups (nested ANOVA, $p < 0.05$). The condition factor fluctuated around 1.1 and 1.2 in both photoperiods between June and November 1997 (Figure 3). The condition factor was not significantly different between groups initially (nested ANOVA, $p > 0.05$), but in general the NL groups had significantly higher condition factor until February 1998. LL groups had significantly better condition in April 1998, while there were no significant differences in August 1998.

There were no significant differences in weight or length at the start or in August 1997 among the groups receiving different levels of exercise under natural or continuous light (nested ANOVA, $p > 0.05$). In September and November 1997, there was a tendency for weight and length to be positively correlated to increasing level of exercise under both natural and continuous light, but the only significant difference was a lower weight in LL-LS compared with the other groups in November 1997 (Tukey HSD, $p < 0.05$). This effect was no longer apparent in the next measurement in January, and there were no significant differences in length or weight between the different exercise levels during the remaining experimental period (nested ANOVA, $p > 0.05$). In August, the low water current groups had significantly lower condition factor than those under medium and high water currents in both light regimes (nested ANOVA, $p < 0.05$). In September 1997, the high water current groups had significantly higher condition factor than the other groups within each light treatment (nested ANOVA, $p < 0.05$). In November 1997, January, February, April, and August 1998, water current did not significantly influence condition factor in either of the light treatments (nested ANOVA, $p > 0.05$).

Liver development

At the start of the experiment in June 1997, HSI was 11.5%, then fluctuated around 10−12% until January−February 1998 (Figure 4). In August 1997, a reduction in HSI was registered in most of the groups, but even though there was a tendency for increasing exercise levels to correlate to lower HSI in each of the light regimes, only the LL-HS showed significantly lower HSI than the other LL groups. The NL groups had significantly higher HSI than the LL groups (nested ANOVA, $p < 0.05$), while gender did not influence HSI. In September, exercise had no effect on HSI within each light regime ($p > 0.05$), and the effect of exercise observed in August had disappeared in

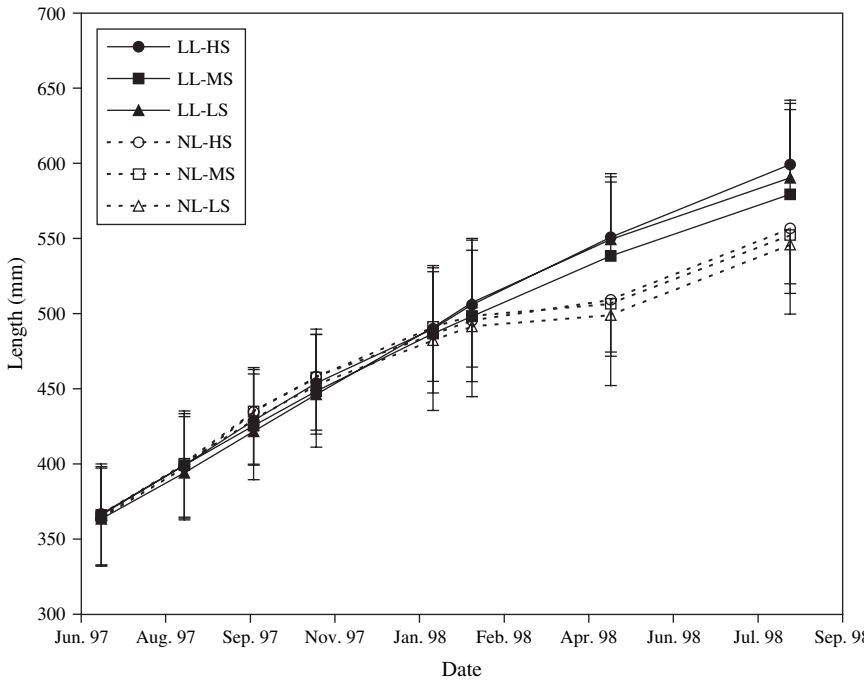

Figure 2. Total length (±s.d.) during the experimental period for pooled sexes exposed to natural (dotted line) and continuous (solid line) light and either high, medium, or low water current.

September, indicating only a temporary effect when the experiment was started. Still the NL groups had higher HSI than the LL groups ($p < 0.05$), while gender did not have any significant influence on HSI. The same pattern was also apparent in November and January. In January, the difference between photoperiod treatments had disappeared. In February, photoperiod did not influence HSI, and under LL, gender or exercise did not influence HSI. NL males had reduced HSIs with increasing level of exercise, and average HSI in the NL-HS group was significantly lower than in males in the NL-LS group and in females in the NL-MS and NL-HS treatments. During the spawning season in April 1998, HSI was significantly reduced in both sexes in the NL groups compared with earlier measurements, as well as compared with the LL groups. The difference was most pronounced in males where NL groups had HSIs of 4−7%, and LL groups had HSIs of ca. 11%. In the LL treatments, neither gender nor exercise significantly influenced HSI, while in the NL groups exercise did not influence HSI, but males showed significantly lower HSI than the females. This difference was no longer apparent in August 1998, when HSIs ranged from 7% to 10% in fish of both sexes and in all groups.

Maturation and gonadal development

More than 95% of the cod reared under NL reached sexual maturity during winter and spring 1998, while no maturing or mature fish were observed in the LL groups throughout the study. Gonadosomatic indices were <1% until September 1997 (Figure 5), before GSI increased in the NL groups from October until January (males) or February (females). The maximum average GSI of NL males was 10.4% in January, and for NL females, maximum GSI was 7.6% in February. This increase in GSI could not be detected in the LL groups, where GSIs in the male and female cod were 0.3% and 1.1%, respectively, on the same dates. From September 1997, the NL groups had significantly higher GSI than the LL groups. In August 1997, the females in the NL treatments had higher GSI than the males, while there were no significant differences between the sexes in November 1997. After November 1997, males had higher GSIs than females. There was no effect of gender in the LL treatments. There were no significant differences in GSI between exercise groups in males or females under LL or NL (two-way ANOVA, $p > 0.05$), even though GSI reached a lower maximum (females) or dropped faster (males) at 0.5 and 1.0 BL s^{-1}. In August 1998, there were no significant effects of photoperiod or degree of exercise on GSI, although females had significantly higher GSI (1.5%, calculated as mean of all treatments) than males (0.6%).

Discussion

Continuous light appeared to arrest sexual maturation in both sexes as determined from GSI and visual inspection

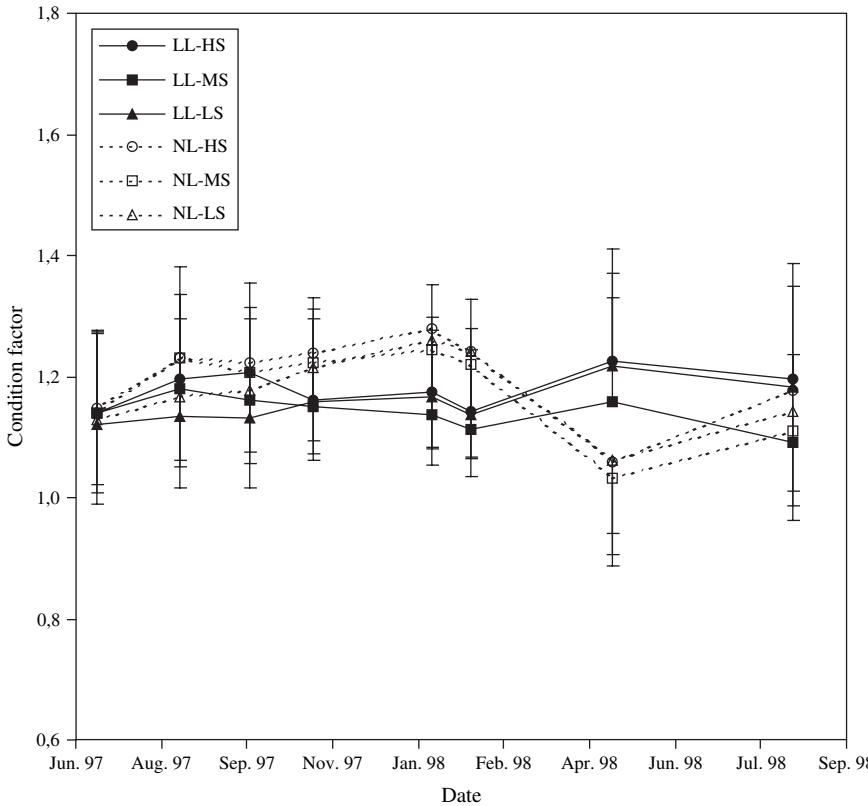

Figure 3. Condition factor (±s.d.) during the experimental period for pooled sexes exposed to natural (dotted line) and continuous (solid line) light and either high, medium, or low water current.

of the gonads, while exercise did not have any significant influence on energy deposition in the liver or gonad development under the experimental conditions used in the present study. A growth-promoting effect of the LL treatment was seen in the current study, in accordance with previous observations on Atlantic salmon (Oppedal *et al.*, 1997; Endal *et al.*, 2000). While the NL groups grew better than the LL groups during the first part of the study, the LL groups were larger than the NL groups from February 1998 onwards. The main cause of these size differences appeared to be weight increase and loss prior to and during spawning in groups kept in natural light, as opposed to LL groups where no spawning was observed during the study. The observed weight loss in Atlantic cod during the spawning season is consistent with previously published work, and is a result of loss of appetite concurrent with a major reallocation of energy from somatic to gonadal growth (Kjesbu *et al.*, 1991; Karlsen *et al.*, 1995; Dahle *et al.*, 2003). Concomitant with weight loss, liver indices were reduced, indicating a mobilization of available energy stores. Liver lipids and muscle protein are the main available energy sources in Atlantic cod (Dambergs, 1964; Jangaard *et al.*, 1967; Eliassen and Vahl, 1982; Black and Love, 1986; Kjesbu *et al.*, 1991; Lambert and Dutil, 1997). Although liver indices were restored to prespawning levels at the end of the experiment in August 1998, average body weights were lower in all NL groups also at this time.

Exercise caused an initial drop in HSI in most experimental groups. However, the exercised cod compensated for the increased energy expenditure within 1 month, and exercise had no marked long-term effects on growth, energy deposition, or investment in reproduction. The results on liver size, sexual maturation, and reproductive investment are in accordance with previous studies, where periodic starvation during the autumn before puberty or restricted feeding a year prior to puberty did not reduce liver sizes to the levels typically found in wild fish. Furthermore, periodic starvation or restricted feeding affected neither investment in reproduction measured as relative fecundity nor age at puberty (Lehman *et al.*, 1991; Kjesbu and Holm, 1994; Karlsen *et al.*, 1995). Only severely restricted feeding affected maturation in repeat spawning cod females (Kjesbu *et al.*, 1991). Farmed cod generally have larger energy deposits than those found in natural populations. As a consequence, liver indices are usually higher in spent farmed cod than in prespawning wild cod stocks (e.g. Eliassen and Vahl, 1982). Fish condition, expressed as size of energy stores, affects reproductive investment in cod

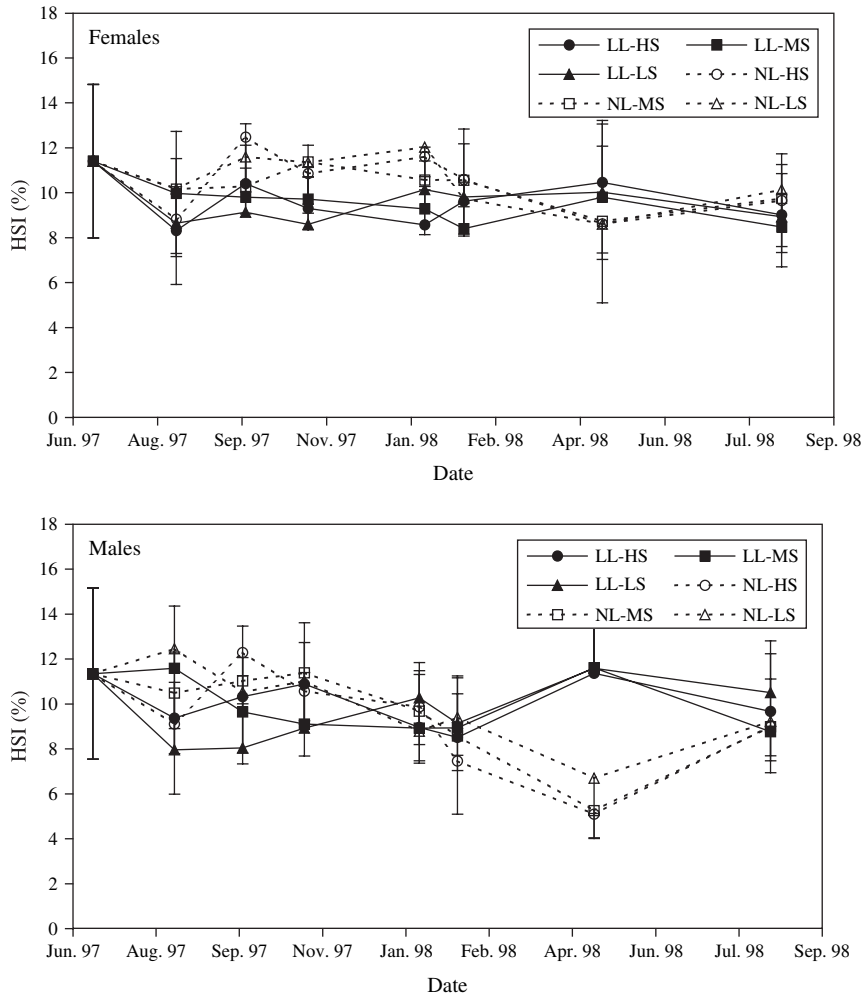

Figure 4. Hepatosomatic index (HSI) (±s.d.) for females and males exposed to natural (dotted line) and continuous (solid line) light and either high, medium, or low water current.

(Kjesbu *et al.*, 1991; Chambers and Waiwood, 1996; Marshall *et al.*, 1999; Lambert and Dutil, 2000; Ouellet *et al.*, 2001). Low energy levels increase the amount of atresia (Kjesbu *et al.*, 1991; Rideout and Burton, 2000) and cause elevated postspawning mortality (Lambert and Dutil, 1997, 2000; Dutil and Lambert, 2000). However, under normal farm conditions, such as in the present study where the fish were fed *ad libitum*, exercise did not appear to affect fish condition or energy allocation patterns. Furthermore, exercise did not affect the proportion of maturing cod, and in a parallel study, it was demonstrated that relative fecundity in the NL groups was not significantly influenced by exercise (Krüger-Johnsen, 1999).

Photoperiod, in contrast, strongly affected the timing of puberty and sexual maturation in agreement with previously published data by our group as well as other workers (Hansen *et al.*, 2001; Davie *et al.*, 2003; Norberg *et al.*, 2004). LL treatment from the summer solstice in the lightproof tanks appeared to arrest gonadal development for at least 8 months in the current study, and no maturation was detected until the experiment was terminated. This agrees with previous studies in indoor tanks (Hansen *et al.*, 2001; Davie *et al.*, 2003). Hansen *et al.* (2001) found that LL treatment from the summer solstice at 15 months of age in indoor tanks allowed oocyte development until the cortical alveoli stage, but further development was arrested. Results of LL treatment on cod in sea cages are not as clear because LL treatment in such systems delays gonadal development and sexual maturation by no more than a few months (Taranger *et al.*, 2006). One could speculate whether the different results seen following LL treatment in sea cages and tanks are the result of differences in swimming activity between the two rearing systems. However, the current results indicate that increased swimming activity and exercise levels in tanks had no effect on gonad development and sexual maturation. Hence, the supposed differences in

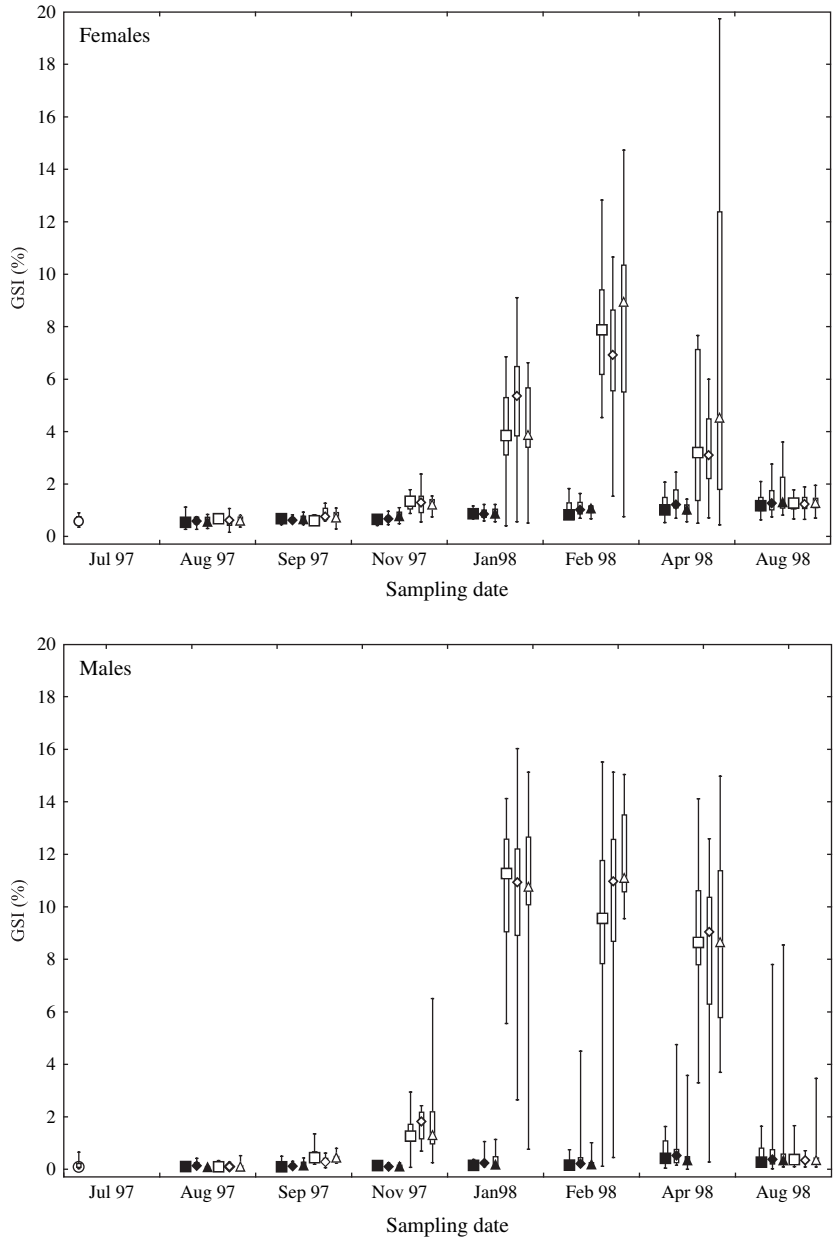

Figure 5. Gonadosomatic index (GSI) for females and males (median, quartile range, and max−min) at the start (open circles), and for those receiving high (squares), medium (triangles), and low water (diamonds) current under LL (open symbols) or NL (filled symbols) at all sampling dates.

exercise levels between sea cages and tanks do not appear to be a major reason for differences observed in maturation following LL treatment in these two systems. A more likely explanation of the differences observed between maturation responses in the two systems may be that, in sea cages, the continuous light treatment is superimposed upon a strong natural photoperiod cycle, while in lightproof or indoor tanks the light is kept at a constant intensity throughout the year, i.e. the fish will experience a true LL in tanks while receiving a combination of LL and ambient light in sea cages. The diel and seasonal changes in light intensity and differences in spectral composition, as well as a weakening of intensity with water depth, may all influence the efficiency of LL treatment in sea cages as compared with lightproof tanks. It is possible that even relatively minor differences in light intensity between day and night experienced in outdoor systems such as sea cages may be critical to the ability of cod to perceive the photoperiod as

continuous or changing and, thereby, affect the results of the photoperiod treatment on gonad development and sexual maturation.

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