Interaction between temperature and photoperiod on growth and feeding of Atlantic cod (*Gadus morhua*): possible secondary effects

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Abstract: Interactions between temperature and photoperiod on growth of Atlantic cod (*Gadus morhua*) juveniles (initial weight 9.1 g) were studied by rearing juvenile cod 3 months under simulated natural photoperiod (LDN) and continuous light (LD24:0) at 7, 10, and 13 °C. Juvenile Atlantic cod exposed to LD24:0 had higher growth rate and better feed conversion efficiency compared with cod reared under LDN. Optimal temperature for growth of juvenile Atlantic cod in the size range 5–50 g was influenced by photoperiod and was estimated to be 12.3 °C under LD24:0 and 15.7 °C under LDN. After termination of the laboratory study, the fish were reared in sea pens at ambient conditions for 17 months. The growth-enhancing effect of LD24:0 could be traced far beyond the duration of the laboratory trial, as the final mean weights in June 2005 of the fish reared at LD24:0 and 13 and 10 °C in the laboratory trial were 8% and 13% higher than those of the respective LDN groups. Our study indicates a physiological mechanism that might be linked to cod migrations, as maximal growth and feeding efficiency will be attained in areas during a season with extended day length or continuous light.

Résumé : L'élevage de jeunes morues franches (*Gadus morhua*) (masse initiale de 9,1 g) durant 3 mois sous une photopériode naturelle simulée (LDN) ou en lumière continue (LD24:0) et à des températures de 7, 10 et 13 °C a permis d'étudier les effets des interactions entre la température et la photopériode sur la croissance. Les jeunes morues franches exposées à LD24:0 ont un taux de croissance plus élevé et une meilleure efficacité de conversion de leur nourriture que les morues gardées à LDN. La température optimale pour la croissance des jeunes morues franches dans l'intervalle de tailles de 5–50 g est influencée par la photopériode et est estimée à 12,3 °C à LD24:0 et à 15,7 °C à LDN. Après la fin de l'étude de laboratoire, les poissons ont été gardés dans des enclos marins aux conditions ambiantes pendant 17 mois. L'effet de stimulation de la croissance par LD24:0 se manifeste bien au-delà des expériences de laboratoire, puisque les masses moyennes finales en juin 2005 des poissons élevés en laboratoire à LD24:0 et aux températures de 13 et de 10 °C étaient respectivement de 8 % et de 13 % plus élevées que celles des groupes LDN correspondants. Notre étude indique l'existence d'un mécanisme physiologique qui pourrait être relié aux migrations des morues, puisque les maximums de croissance et d'efficacité alimentaire sont atteints dans des zones où il y a une saison de lumière continuelle ou de photophase étendue.

[Traduit par la Rédaction]

Introduction

Information about the effect of photoperiod on growth dynamics in early juvenile Atlantic cod (*Gadus morhua*) is limited. In wild populations of Atlantic cod, seasonal variations in growth rate have been demonstrated (e.g., Schwalme and Chouinard 1999), although the changes caused by photoperiods per se are difficult to isolate from other concurrent changes in environmental factors such as temperature. Under altered photoperiods, fish are expected to adjust gradually to a new photoperiod regime by regulating feeding activity, growth, and food utilization (Boehlert 1981; Woiwode and Adelman 1991; Bromage et al. 2001). Photoperiod manipulation has been shown to enhance growth in several species. A growth-promoting effect of extended photoperiods has been demonstrated in juvenile Atlantic salmon (*Salmo salar*) (e.g., Stefansson et al. 1989; Solbakken et al. 1994) and

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Pacific salmonids (*Oncorhynchus* spp.) (e.g., Clarke et al. 1981). This also seems to be the case for splitnose rockfish (*Sebastes diploproa*) (Boehlert 1981), turbot (*Scophthalmus maximus*) (Imsland et al. 1995, 1997, 2003), Atlantic halibut (*Hippoglossus hippoglossus*) (Simensen et al. 2000; Imsland and Jonassen 2005), and early Atlantic cod juveniles (Folkvord and Otterå 1993), although the response does not appear to be as pronounced as that observed in salmonids. A delayed response to photoperiod at low temperature has been shown in Atlantic salmon (Solbakken et al. 1994), and Clarke et al. (1978) concluded that changes in growth rate resulting from photoperiod were apparent sooner at higher temperatures owing to the rate-controlling effect of temperature. In contrast, Imsland et al. (1995) found that the relative response and duration of the growth enhancement of continuous light were longer at suboptimal temperature in turbot. Similarly, Jonassen et al. (2000*a*) found a significant interaction between temperature and light, suggesting a relatively stronger growth-enhancing effect of continuous light at lower temperature.

Many of the world's most commercially important cod populations perform extended seasonal migrations (up to 1000 km; Comeau et al. 2002*a*). In spring, migratory cod generally move from offshore to inshore areas (Lear and Green 1984; Comeau et al. 2002*a*, 2002*b*) where prey is abundant (e.g., Lambert and Dutil 1997). To ensure that the evolutionary benefits of migration outweigh the risks, a safe and reliable control mechanism must be in place so that migratory movements are initiated at the appropriate times within the physiological and environmental cycles (Comeau et al. 2002*a*). Off the Norwegian coast, coastal cod live their whole life close to the coast, while northeast Arctic cod spawn in Norwegian coastal areas in spring but feed in the Barents Sea – Svalbard region. Northeast Arctic cod perform yearly migrations of several thousand kilometres and it is unclear whether this is driven by photoperiod conditions (Stensholt 2001). However, such photoperiod-related migration has been indicated off the eastern coast of Canada (Comeau et al. 2002*a*, 2002*b*).

The purpose of this study was to investigate the possible interactive effect of photoperiod and temperature on both short- and long-term growth in juvenile Atlantic cod. By quantifying the possible gain in terms of increased growth, feed intake, and improved feed efficiency of cod reared at continuous light, we hope to gain more understanding of the underlying mechanism behind life history and migration strategies.

Materials and methods

Fish material and rearing conditions

The eggs were obtained from two commercial cod juvenile producers. The first group was attained from a cod hatchery in western Norway (59°50′N) and transported to the facilities of the University of Bergen where they were incubated. The broodfish were wild caught in the area around Bømlo (western Norway) in 2003 and reared in 40 m^3 tanks at simulated natural photoperiod and temperature of 6–8 °C (seawater pumped from 160 m depth). The mean weight of the broodfish was approximately 7 kg (range 5–18 kg). The eggs hatched on 28 March and the larvae were subsequently transferred to a 500 L tank with a constant temperature of 7.8 °C. The larvae were reared under continuous light, fed fresh filtered natural zooplankton (gradually increasing size fraction from 80 to 1000 μm), and weaned on a commercial formulated feed (Marin 030 and 050; Ewos A/S, Bergen, Norway) containing 60% protein, 12% fat, and 12% carbohydrates. On 20 June 2003, the juveniles were brought to the Industrial and Aquatic Laboratory (ILAB) at the Bergen High Technology Centre and reared at 10 °C and under a simulated natural photoperiod (LDN, 60°N) until the start of the study. This group of fish was mixed with an equal number of fish originating from another cod hatchery from western Norway (61°40′N). The broodfish were wild caught in the area around Møre (western Norway) in 2003 and reared in 70 m^3 tanks under LDN and temperature of 6–8 °C (seawater pumped from 100 m depth). The mean weight of the broodfish was approximately 15 kg (range 7–22 kg). The eggs were incubated at 7.0 °C, hatched on 25 March, and kept at 8–10 °C (gradual increase) during the first weeks of development. The larvae were reared under constant 16 h light : 8 h darkness (LD16:8), fed (size at start-feeding approximately 5 mm) enriched (Nannochloropsis Instant Algae®) rotifers for 35 days (prey density 2000 rotifers·L^{-1} for the first 10 days and then 4000 rotifers·L^{-1}), and then cofed for 10 days with commercial dry feed (Ewos Marin 030 and 050). On 22 June, the fish were transported to the ILAB and reared under the same conditions as described above. A more detailed description of the larvae and early juvenile protocol is given in Imsland et al. (2006).

After arrival at ILAB, the juveniles from the different producers were tagged with visible implant fluorescent elastomer tags (Northwest Marine Technology, Shaw Island, Washington), and thereafter, the fish (n = 1347) from the two groups were mixed and distributed randomly into 12 experimental tanks. Equal numbers of fish from the two producers were placed in each tank. The 1 m^2 square, grey, covered fiberglass experimental tanks had a rearing volume of 400 L and a bottom outlet. Seawater with a salinity of 33.5‰ (±0.2‰) was pumped from 90 m depth. Water flow was set to 10 L·min^{-1} for all experimental tanks. Oxygen saturation was measured weekly in the effluent (i.e., bottom outlet) water of all tanks and was higher than 80% at all times. A 36 W fluorescent daylight tube (Osram L36 W/12 Lumilux Deluxe Daylight; Osram GmbH, München, Germany) integrated in the tank cover provided light. Photon irradiation measured at the bottom of the tanks was approximately 5 μmol·m^{-2}·s^{-1}. During both the acclimation period and the experiment, the juveniles were fed a commercial dry diet (Marin 10 and 20, Ewos AS; 55% protein, 12% fat, 11% carbohydrate, gross digestible energy 20.4 MJ·kg^{-1}). Feed was provided in excess for 2 h daily (0800–0900 and 1400–1500). Pellet size (2 and 3 mm) was adjusted during the experiment, depending on fish size, with an introduction of 3 mm pellets beginning 14 October. Uneaten pellets were collected after each feeding (no later than 30 min after each feeding pulse) by filtering the outlet water with a fine mesh and counted to estimate feed intake and feed conversion efficiency. Our observations showed that the amount of feed broken down was negligible in the short time from feeding to sampling and that this sampling method gave an accurate estimate of the amount of feed eaten.

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Experimental design

The growth study was carried out from 8 September until 12 December 2003. On 25 August 2003, in preparation for the study, a subgroup within each tank (n = 44–46 in each tank, total n = 538) were tagged intraperitoneally with Trovan® passive transponder tags and gradually acclimated over 1 day to 7 and 13 °C (eight tanks) or kept at 10 °C (four tanks). At each temperature, one group was exposed to LDN for Bergen (60°25′N) generated by a computer program (Lysstyr v. 2.0; Hansen 1990), including twilight periods, whereas the other group was exposed to continuous light (LD24:0). Each photoperiod–temperature regime consisted of two replicate tanks, so our setup is a three-way nested design where temperatures and photoperiods are crossed and replicates nested within temperatures and photoperiods. The temperature in all groups was measured twice daily and remained within ±0.2 °C (SD) of that prescribed. All fish were anaesthetized (0.05 g metacain·L^{-1}) and weighed individually (0.1 g) at 22–28 day intervals during the experiment.

After termination of the laboratory trial, all individually tagged fish (n = 597) were acclimated to 10 °C and transported by truck on 15 January 2004 to the production site of Marine Harvest at Tustna (North Trøndelag County, western Norway). Here, the fish were held in a land-based tank (8 m in diameter, 85 m^3 volume) until 25 May 2004 when they were transferred to a sea site at Smøla (western Norway, 63°31′N). The fish were reared at ambient temperatures (range mean temperatures 15 °C in August to 5 °C in March) together with 7500 other (untagged) cod in one sea pen (40 m in diameter, 7 m deep, 1000 m^3 volume). Mean weight at the start (all fish) was 172 g and the total biomass in the sea pen was approximately 9000 kg at the start. The fish were hand-fed five times a week using a commercial formulated feed from Dana Feed (Dan-Ex 1562 containing 15% fat and 58% protein). On 29 June 2005, the weight of 105 tagged fish from the laboratory study was measured. The total number of fish in June 2005 was 7700 with an average weight (all fish) of 1200 g.

Data analysis and statistical methods

Total feed consumption (C_T) was calculated as total feed supplied minus the total remaining feed. The C_T was calculated on a daily basis and then summarized for each of the four growth periods. Daily feeding rate (F%) was calculated as

$$F\% = 100[C/((B_1 + B_2)/2)](t_2 - t_1)^{-1} \quad (1)$$

where C is feed consumption (g) in the period and B_1 and B_2 are fish biomass (g) on days t_1 and t_2, respectively. Feed conversion efficiency (FCE) was calculated as biomass gain per unit weight of feed consumed:

$$\text{FCE} = (B_2 - B_1)/C \quad (2)$$

Specific growth rate (G) was calculated according to the formula of Houde and Schekter (1981):

$$G + (e^g - 1)100 \quad (3)$$

where the instantaneous growth coefficient g is

$$g = (\ln W_2 - \ln W_1)(t_2 - t_1)^{-1} \quad (4)$$

where W_2 and W_1 are wet weight (g) on days t_2 and t_1, respectively.

All statistical analyses were performed with STATISTICA™ 6.1 (StatSoft Inc., Tulsa, Oklahoma). To assess normality of distributions, a Kolmogorov–Smirnov test was used and homogeneity of variances was tested using the Levene F test. A three-way ANOVA (Zar 1984) was applied to calculate the effect of different photoperiods and temperatures on mean weights, specific growth, feed consumption, daily feeding rate, and feed conversion efficiency, where the replicates are nested within the photoperiods and temperatures. The model equation of the nested ANOVA has the form

$$X_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_{ij} + C_{ijk} + \varepsilon_{ijkl} \quad (5)$$

where μ is the general level, α_i is the treatment effect of temperature i, β_j is the treatment effect of photoperiod j, γ_{ij} is the effect of interactions between temperature α_i and photoperiod β_j, C_{ijk} is the contribution caused by replicate (here, tank) k in group ij, and ε_{ijkl} is the error term. Significant ANOVAs were followed by a Student–Newman–Keuls multiple comparison test to locate differences among treatments (Zar 1984). For weight data of fish in sea pens, we used a Tukey honestly significant difference (HSD) unequal N test to locate differences, as the number of fish was unequal between the groups.

Individual growth trajectories were analysed using a growth curve analysis (GCM) multivariate analysis of variance (MANOVA) model (Timm 1980; Chambers and Miller 1995). The model equation of the GCM has the form

$$\mathbf{Y}(n \times p) = \mathbf{X}(n \times q)\,\mathbf{B}(q \times p) + \mathbf{E}(n \times p) \quad (6)$$

where $\mathbf{Y}(n \times p)$ are the growth at age vectors

$$\mathbf{y} = (y_1, y_2, \ldots, y_p) \quad (7)$$

for each p (age) measurement on n individual fish, $\mathbf{X}(n \times q)$ is the design matrix or the set of extraneous variables measured for each individual, i.e., q = age p+ temperature i + photoperiod j + replicate k (i = 7, 10, 13 °C; j = LDN, LD24:0; k = replicate a, replicate b), $\mathbf{B}(q \times p)$ is the matrix of parameters estimated by the model, and $\mathbf{E}(n \times p)$ is the matrix of deviations for each individual from the expected value of $\mathbf{Y} = \mathbf{XB}$.

Specific growth in relation to photoperiods was analysed with a parabolic regression (Zar 1984) where growth was regressed against temperature for the two photoperiod groups. The regression was made using the combined growth rates of all tagged fish at each temperature for the photoperiod groups. Optimal temperatures for growth ($T_{opt}G$) were calculated as the zero solution to the first derivative of the parabolic regression equations, i.e., the solution of

$$G = aT^2 + bT + c \text{ or } dG/dT = 0 \rightarrow T_{opt}G = -b/2c \quad (8)$$

where G is specific growth rate, T is temperature (°C), and a, b, and c are constants determined by the regression. The asymptotic SE of the mean for $T_{opt}G$ was calculated based on individual growth data. As we were limited to only three temperatures when calculating $T_{opt}G$, a jackknife procedure (Shao and Tu 1996) was applied to generate new data sets so

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that that bias of the estimator ($T_{opt}G$) could be reduced by calculating several jackknife estimators.

Results

Mortality

Total mortality during the tank study was 2.0% (11 fish). No systematic trend was found, as mortality occurred in all rearing units, except the 7 °C-LD24:0 group. Although not significantly different, overall mortality was higher under LDN, as eight of the dead fish were from the LDN groups and three from the LD24:0 group ($\chi^2_1 = 3.2$, $p > 0.07$). At 7 °C, mortality was higher in the LDN group ($\chi^2_1 = 5.4$, $p < 0.05$). A size-dependent mortality was found in the LDN group, as the dead fish were significantly smaller than the surviving fish (one-way ANOVA, $p < 0.05$). No size-dependent mortality was seen for the LD24:0 groups (one-way ANOVA, $p > 0.70$).

Short-term effect of photoperiod on growth

The overall initial mean weight (SD) was 9.1 (2.7) g and did not differ (three-way nested ANOVA, power $(1 - \beta) > 0.7$) (Fig. 1) between the photoperiod groups. From October onwards, the 13 °C-LD24:0 group had the highest mean weight (three-way nested ANOVA, $p < 0.05$) (Fig. 1), whereas no differences were found between the photoperiod groups at 7 °C. Accordingly, a significant interaction between temperature and photoperiods (three-way nested ANOVA, $p < 0.05$) was found from October until December. The final mean weights in December 2003 of the LD24:0 groups at 13 and 10 °C were 15% and 11% higher, respectively, than those of the LDN group.

The fish reared under the different photoperiod regimes differed in their growth patterns and the GCM analyses revealed differences between the individual growth trajectories of the photoperiod regimes ($MANOVA_{(PHOTOPERIOD)}$, Wilk's $\Lambda_{4,529} = 0.88$, $p < 0.001$) and between the temperatures ($MANOVA_{(TEMPERATURE)}$, Wilk's $\Lambda_{8,1058} = 0.38$, $p < 0.001$). Growth in the different time periods varied highly (Fig. 2), but in general, significant differences were seen between the LDN and LD24:0 groups at each temperature from late October onwards (Student–Newman–Keuls, $p < 0.05$) (Fig. 2). Accordingly, the LD24:0 groups had higher overall specific growth rate compared with the respective LDN groups at all temperatures (Fig. 2). The relative difference between the overall growth rates under LDN and LD24:0 varied between the temperatures and was highest at 10 °C (11% difference), and consequently, an interaction between temperature and photoperiod was seen ($MANOVA_{PHOTOPERIOD \times TEMPERATURE}$, Wilk's $\Lambda_{8,1058} = 0.95$, $p < 0.01$). A significant interaction effect between temperature and photoperiod on growth was found in the first and third experimental periods (Fig. 2).

When growth rates were plotted against temperature for the two photoperiod groups, the resulting parabolic regressions (Fig. 3) indicated that the temperature optimum for maximum growth in juvenile cod ($T_{opt}G \pm$ SE) varied between photoperiods and was estimated to be 15.7 ± 0.5 °C for the LDN group and 12.3 ± 0.2 °C for the LD24:0 group.

Feed intake, feeding rate, and feed conversion efficiency

The overall mean feed consumption (C_T) and daily feeding rate ($F\%$) did not differ between the photoperiod groups at each temperature (three-way nested ANOVA, $p > 0.3$) (Table 1). However, the LD24:0 groups had higher feed conversion efficiencies compared with the LDN groups at all temperatures (Student–Newman–Keuls test, $p < 0.05$). Feed consumption and daily feeding rate differed between temperature regimes (Table 1). The 13 °C group had the highest feed consumption and the 7 °C group the lowest consumption. Across temperatures, the 7 °C group had the lowest $F\%$, whereas the 10 and 13 °C groups showed similar daily feeding rates.

Long-term effect of photoperiod on growth

The mean weight of fish reared at different temperatures and photoperiods during the early juvenile stages differed following the 17-month commercial rearing period (Tukey HSD unequal N test, $p < 0.05$) (Fig. 4). On 29 June 2005, the mean weights (±SE) of the fish previously reared under LD24:0 at 10 and 13 °C were highest (1.70 ± 0.04 kg, n = 18 and 1.69 ± 0.08 kg, n = 22, respectively) followed by the 13 °C-LDN fish (1.56 ± 0.05 kg, n = 21). The fish reared at 7 °C (both groups: 1.50 ± 0.06 kg, n = 11 and 15 for former LD24:0 and LDN groups, respectively) in the laboratory trial and the fish reared under LDN and at 10 °C were significantly smaller (1.48 ± 0.08 kg, n = 18) than the fish reared under LD24:0 at 10 and 13 °C in the laboratory trial.

Discussion

Our data show that juvenile Atlantic cod exposed to continuous light have higher growth and better feed conversion efficiency than cod reared on simulated natural photoperiod during autumn. Earlier studies have addressed the effect of continuous light on survival and growth of Atlantic cod larvae (Puvanendran and Brown 2002), short-term effects on 1–2 g juveniles (Folkvord and Otterå 1993), and effects on sexual maturation and growth of adult cod (Hansen et al. 2001; Karlsen et al. 2006; Taranger et al. 2006). However, studies on the effects of photoperiod on survival, growth, and feed conversion efficiency in early juvenile (3–100 g) Atlantic cod have been absent until now. Puvanendran and Brown (2002) found that cod larvae grew and survived better under continuous light compared with LD18:6 and LD12:12 regimes. The combination of rearing the larvae at high light intensities (2400 lx) and continuous light increased encounter rate and improved capture success of the larvae towards its prey. For adult cod, continuous light could, theoretically, have a dual effect on growth: a direct growth-enhancing effect and a secondary effect by arresting gonad development and inhibiting spawning. Earlier studies with adult cod were unable to differentiate whether the growth gain is due to direct photostimulation of growth or inhibition of sexual maturation allowing continued growth (e.g., Hansen et al. 2001; Karlsen et al. 2006; Taranger et al. 2006). In the present study with immature juvenile cod, a direct growth-enhancing effect was demonstrated. Such a direct growth-promoting effect of long days or continuous light has been found in Atlantic salmon (Kråkenes et al. 1991; Hansen et al. 1992),

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Fig. 1. Mean (±SE) weight for individually tagged Atlantic cod (*Gadus morhua*) reared at different photoperiods and temperatures. The vertical line indicating SE may be obscured by the symbol. Different letters indicate statistical differences (three-way nested ANOVA, $p < 0.05$) between the experimental groups, with *a* as the highest value. The values for two replicates are combined, $n = 80–82$ for each mean value. ns, not significant;an asterisk indicates a significant interaction between temperature and photoperiod regime. Squares, 7 °C; triangles, 10 °C; circles, 13 °C; open symbols and broken line, LDN; solid symbols and solid line, LD24:0.

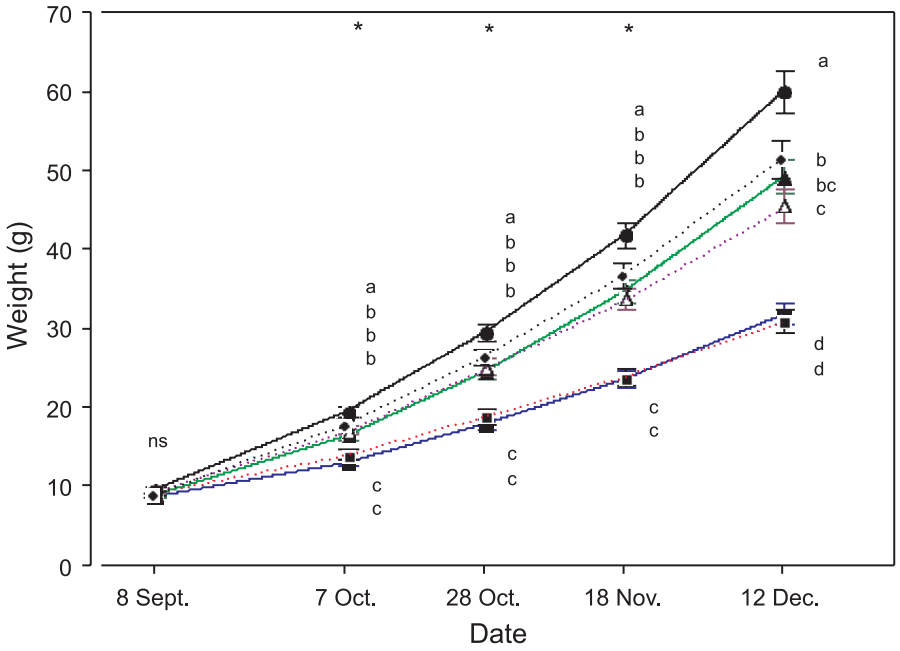
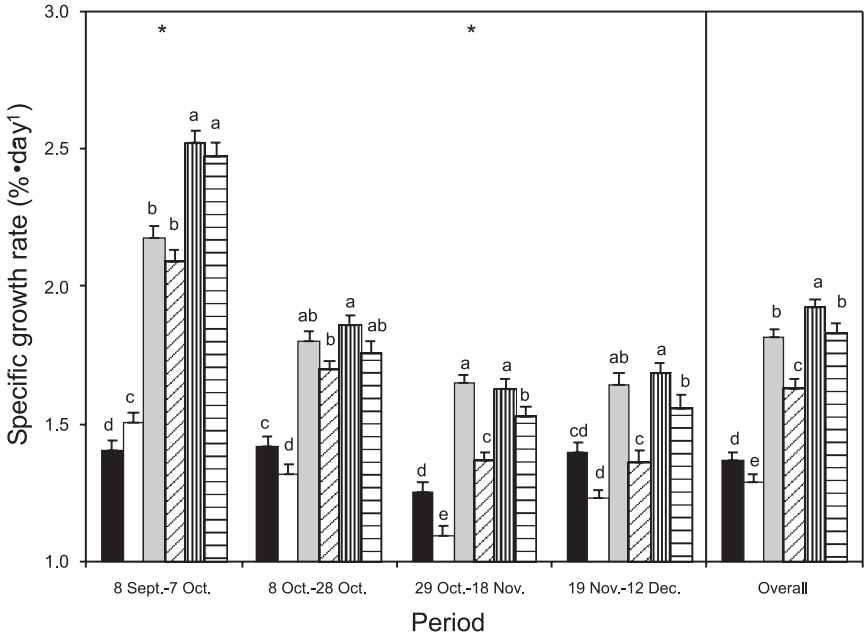


Fig. 2. Mean specific growth rates of individually tagged Atlantic cod (*Gadus morhua*) reared at different photoperiods and temperature during the experimental period. Vertical whiskers indicate SE. Different letters denote significant differences (Student–Newman–Keuls test, $p < 0.05$) between the experimental groups, with *a* as the highest value. The values for two replicates are combined, $n = 80–82$ for each mean value. ns, not significant; an asterisk indicates a significant interaction between temperature and photoperiod regime. Solid bars, 7 °C-LD24:0; open bars, 7 °C-LDN; grey bars, 10 °C-LD24:0; hatched bars, 10 °C-LDN; vertical lined bars, 13 °C-LDN24:0; horizontal lined bars, 13 °C-LDN.



Atlantic halibut (Simensen et al. 2000; Imsland and Jonassen 2005), and turbot (Imsland et al. 1995, 1997, 2003). The present study is the first to verify this effect in the early juvenile stages of cod. Taken together, the data from studies with larval (Puvanendran and Brown 2002), juvenile (this study), and adult cod (Davie et al. 2003; Karlsen et al. 2006;

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Fig. 3. Changes in specific growth rate (SGR) of juvenile Atlantic cod (*Gadus morhua*) with temperature for two different photoperiod regimes. The lines represent the least squares second-order polynomial fit to the data: SGR = $aT^2 + bT + c$, where T is temperature and a, b, and c are constants determined by the regression. Solid line, LD24:0; broken line, LDN. Vertical lines indicate SE of the mean, n = 83–90 for each data point. For the two photoperiod groups, optimum temperature for growth ($T_{opt}G$) indicated by the solid line (LD24:0) and broken line (LDN) line was calculated from the first-order derivative of the parabolic regressions (i.e., when dG/dT = 0). Equations for the two photoperiods: LD24:0, SGR = $-0.019T^2 + 0.477T - 1.035$; LDN, SGR = $-0.008T^2 + 0.248T - 0.069$.

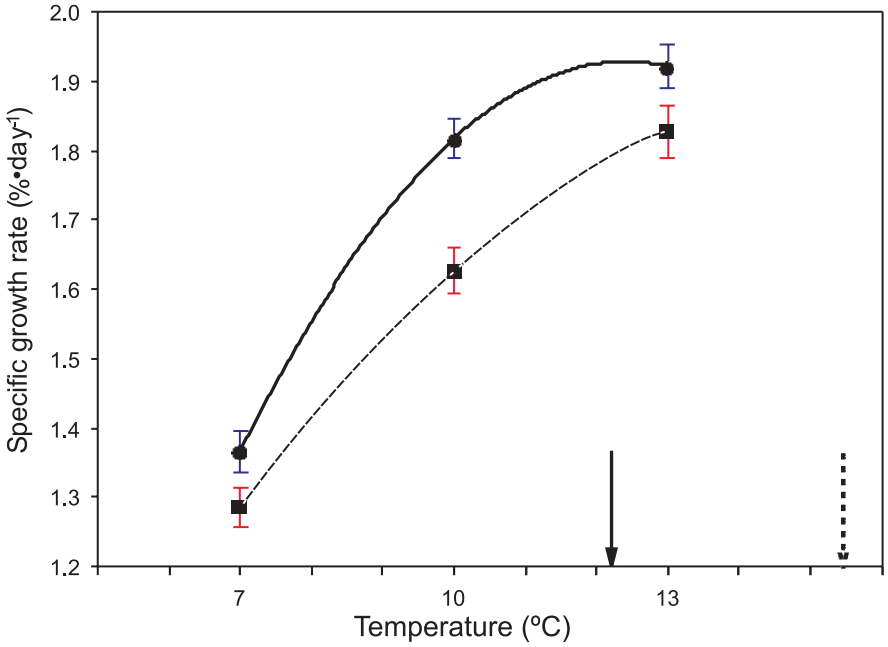

Table 1. Feed consumption (C_T), daily feeding rate (F%), and feed conversion efficiency (FCE) of juvenile Atlantic cod (*Gadus morhua*) reared under three temperature regimes and two photoperiods.

Temperature (°C)	Photoperiod	C_T (g wet weight)	F%	FCE
7	LDN	428.3 (41.4)*c*	1.01 (0.15)*b*	1.10 (0.13)*b*
	LD24:0	485.9 (102.6)*c*	1.12 (0.11)*b*	1.22 (0.04)*a*
10	LDN	655.3 (76.8)*b*	1.31 (0.22)*a*	1.14 (0.09)*b*
	LD24:0	752.4 (130.4)*b*	1.41 (0.25)*a*	1.22 (0.07)*a*
13	LDN	883.7 (149.8)*a*	1.46 (0.27)*a*	1.14 (0.06)*b*
	LD24:0	926.3 (207.1)*a*	1.48 (0.25)*a*	1.24 (0.05)*a*

Note: Results are given as mean (SD) (n = 8) for each factor combination. Different letters denote significant differences (three-way nested ANOVA, $p < 0.05$) between temperature and photoperiod treatments.

Taranger et al. 2006) all highlight the positive short- and long-term effect of continuous light on growth.

Interacting effects of light and temperature are often caused by a shift in the optimum temperature for growth with a changing photoperiod. A positive relationship between day length and optimum temperature for growth is evident in most investigations of freshwater fish (Kilambi et al. 1970; Woiwode and Adelman 1991; Solbakken et al. 1994). Most reports on temperate marine species, however, differ from this pattern. No seasonal differences have been found in the final temperature preference of European plaice (*Pleuronectes platessa*) (Zahn 1963) or the estuarine goby (longjaw mudsucker) (*Gillichthys mirabilis*) (DeVlaming 1971). The same was evident for optimum temperature for growth in Atlantic halibut (*Hippoglossus hippoglossus*) (Hallaråker et al. 1995) and splitnose rockfish (*Sebastes diplopora*) (Boehlert 1981). A possible reason for the apparent lack of a seasonal temperature acclimation in marine species could be the relatively stable seasonal temperature regime in the sea compared with fresh water, thus reducing the selection pressure for such adaptations. Moreover, in Atlantic halibut (Jonassen et al. 2000*b*), turbot (Imsland et al. 2000), and Atlantic silverside (*Menidia menidia*) (Conover 1990; Conover and Present 1990), countergradient growth compensation, rather than temperature acclimation, has been suggested as an adaptation to a temperature-restricted growing season at higher latitudes. Our data point out the possibility of a changed optimum temperature during rearing under continuous light as an explanation of the relatively stronger growth-enhancing effect of continuous light at high temperatures (although it should be noted that our model is derived from three data points from each photoperiod and hence requires confirmation). Our calculated optimal temperature for growth is higher (15.7 °C) for the LDN group compared

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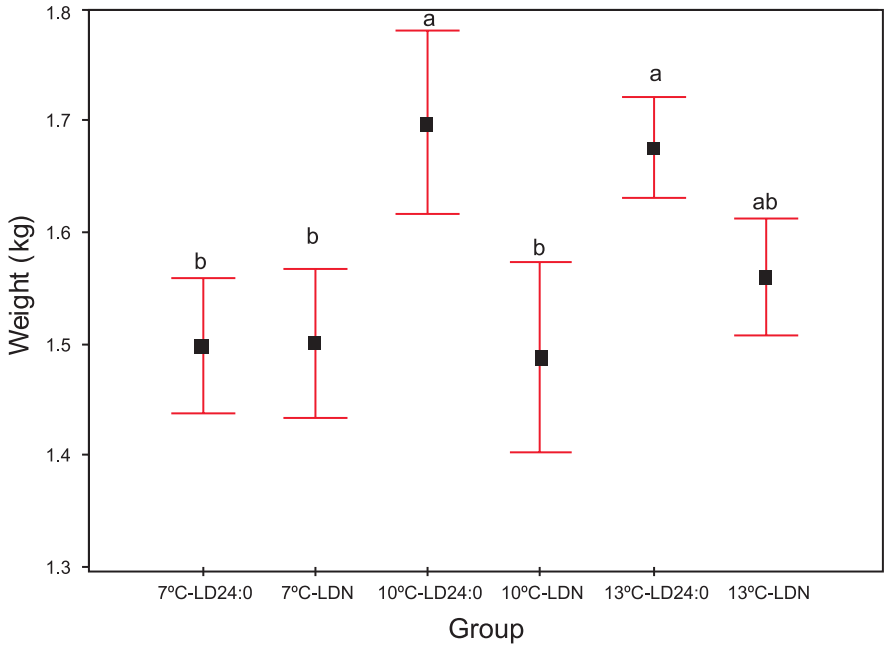
Fig. 4. Mean weight of Atlantic cod (*Gadus morhua*) reared under different temperature and photoperiod regimes during the early juvenile stage and then reared in sea pens at ambient conditions for 17 months. Different letters indicate statistical differences (Tukey's HSD unequal *N* test, $p < 0.05$), with *a* as the highest value, $n = 11–22$ for each mean value.



with the LD24:0 group (12.3 °C). It is possible that this temperature–photoperiod growth model may vary in relation to genotype. In a parallel study, Imsland et al. (2005) found significant interaction between haemoglobin genotypes and photoperiods, demonstrated by the variation in genotype response towards photoperiod treatment. At both temperatures investigated (10 and 13 °C), the highest growth rates were found for the *Hb-I(2/2)* genotype at LD24:0, whereas the lowest overall mean growth rates were found for the same genotype reared under LDN. Conversely, the *Hb-I(1/1)* genotype displayed the fastest specific growth rates in the LDN groups at both temperatures. The data of Imsland et al. (2005) clearly suggest that the genetic composition must be considered in order to increase the effect of photoperiod treatment in Atlantic cod.

It has been shown that bigger size-at-age found in the northeast Arctic cod when compared with Nova Scotian cod in Canada is linked with photoperiod, indicating a possible light-limited feeding opportunity in southern cod stocks (Suthers and Sundby 1996). Our data indicate a more direct effect, as continuous light was found to both enhance growth and improve feed conversion under conditions where feed was not limiting. The data of Suthers and Sundby (1996) together with our findings suggest that photoperiod could be a powerful driving force behind cod migrations, where fish could maximize their size-at-age by northbound migration during summertime in the Northern Hemisphere. Such photoperiod-related migration has been indicated off the eastern coast of Canada (Comeau et al. 2002*a*, 2002*b*). Clearly, there are other proximal cues that govern the migratory behaviour of cod (Stensholt 2001; Comeau et al. 2002*a*, 2002*b*), but our data point to an interesting secondary effect of seeking out high-latitude areas during summer. Foraging in such areas (where light is continuous during summer) will have a direct growth-enhancing effect, thus shortening the time the fish needs to achieve a critical size to survive the first winter (Shuter and Post 1990; Conover 1992 and references therein).

Based on our data, it seems that continuous light has similar effect in Atlantic cod as found for salmonids, where the growth-enhancing effect of extended photoperiods and continuous light is more prominent at near-optimal temperatures (Clarke et al. 1978; Solbakken et al. 1994). Earlier findings in other marine species, e.g., Atlantic halibut and turbot, contrast our findings on Atlantic cod. The findings of Jonassen et al. (2000*a*) suggest that the magnitude of the effect of continuous light on growth is inversely related to temperature in Atlantic halibut. Further support for this is found in studies on juvenile turbot (Imsland et al. 1995, 1997) demonstrating that the growth-promoting effect of continuous light can be stronger at low temperatures than at the near-optimum temperature for the species. These findings on Atlantic halibut and turbot contrast our data where the growth-enhancing effect of continuous light increased with increasing temperature.

Photostimulation may affect fish growth through better food conversion efficiency and not just through stimulated food intake (see review by Boeuf and Le Bail 1999). In a recent study of Atlantic salmon, Handeland et al. (2003) showed that constant light stimulated growth through increased food consumption (but not improved food conversion efficiency) in both wild and selected strains, concurrent with an increase in growth hormone, while the selected strains showed better food conversion than the wild strains under both LD24:0 and LDN. In contrast, Jonassen et al. (2000*a*) reported improved food conversion efficiency (but no difference in food consumption) in juvenile halibut subjected to continuous light at two temperatures. Accordingly, it appears that nonsalmonids adjust to extended photoperiods by displaying higher feeding activity, growth, and food utilization (Boehlert 1981;

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Woiwode and Adelman 1991). Boehlert (1981) found positive effects of photoperiod on growth in splitnose rockfish, where constant LD16:8 resulted in enhanced growth compared with LD12:12 and was probably related to a greater scope for growth owing to a lower standard metabolic rate. In the current trial, Atlantic cod reared at continuous light had higher growth in conjunction with higher feed conversion. In contrast, food consumption and feeding rate followed the increase in temperature and were independent of photoperiod.

The observed growth response following a sudden increase in photoperiod was delayed by at least 21 days after the exposure of the fish to continuous light, and in fact, an initial negative effect of continuous light was seen at 7 °C in this period. The same pattern has been reported in Atlantic salmon subjected to continuous additional light superimposed on natural photoperiod in seawater (Hansen et al. 1992; Endal et al. 2000) and in Atlantic halibut (Simensen et al. 2000), suggesting that the fish in seawater require some time to adapt to changes in photoperiod. Moreover, the previous photoperiod history of the fish may have an important influence on the growth response to a change in light regime (Hoar 1988; Clarke et al. 1989), with a decrease in photoperiod having a growth-depressing effect in several species (e.g., Skilbrei et al. 1997). This could explain some of the differences seen between the two light regimes, as the LDN group experienced diminishing light as the daylight period was reduced from approximately 12 h in September to 7 h in December.

A finding in this study that could have an important implication for the aquaculture sector is the advantage of rearing the fish at optimal temperatures and under continuous light during the juvenile period, as size differences established at this stage may be maintained in the adult fish (Imsland et al. 2006). Similar findings have been observed for wild juvenile northeast Arctic cod where significant size correlations are documented between year-classes and the basis for these relative size differences are formed during the first half year of life (Ottersen et al. 2002). In contrast, recent findings (Sæther 2005) have indicated that moving juvenile cod from different rearing temperatures (between 8 and 15 °C) to low temperature (3 °C) will lead to growth reduction in all groups that will obliterate the short-term gain of rearing juvenile cod at elevated temperatures. In our study, the tagged fish were acclimatized to 10 °C before transport to commercial ongrowing in northwestern Norway and moved to sea pens when sea temperature was approximately 7 °C. Size differences after 17 months in sea pens were slightly reduced, but the general picture was that differences in the juvenile stage could be traced throughout the adult stage. This long-term growth effect could have a positive effect on the commercial aquaculture of Atlantic cod. By applying optimal combinations of temperatures and photoperiods during the juvenile phase in land-based farms, the farmer may be able to produce more biomass on a given time scale of a commercial-sized fish.

Earlier studies have shown that increased light intensity and (or) photoperiod may decrease the incidence of early cannibalism (Baras et al. 1999, 2000). In vindu (*Heterobranchus longifilis*), cannibalism was found to be essentially nocturnal (Baras et al. 1999) and decreased with increased day length, with the lowest cannibalism seen in groups reared under continuous light. Whether this is the case in early juvenile Atlantic cod is unknown. The present data show that total mortality (cannibalism and other causes) was slightly higher in the LDN group compared with the continuous light group. A more detailed study of the interplay between light and cannibalism is needed to verify, or falsify, whether continuous light may reduce the incidence of cannibalism in early juvenile cod.

In conclusion, the present study shows that Atlantic cod exposed to continuous light had higher growth and better feed conversion efficiency and were significantly larger than cod reared under a simulated natural photoperiod. The effect is more profound at near-optimal temperatures, and these differences in size as result of previous temperature and light regime are maintained at later stages. These findings may have important consequences for optimization of the commercial production of Atlantic cod and may increase our knowledge of proximal cues for migrations in Atlantic cod.

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